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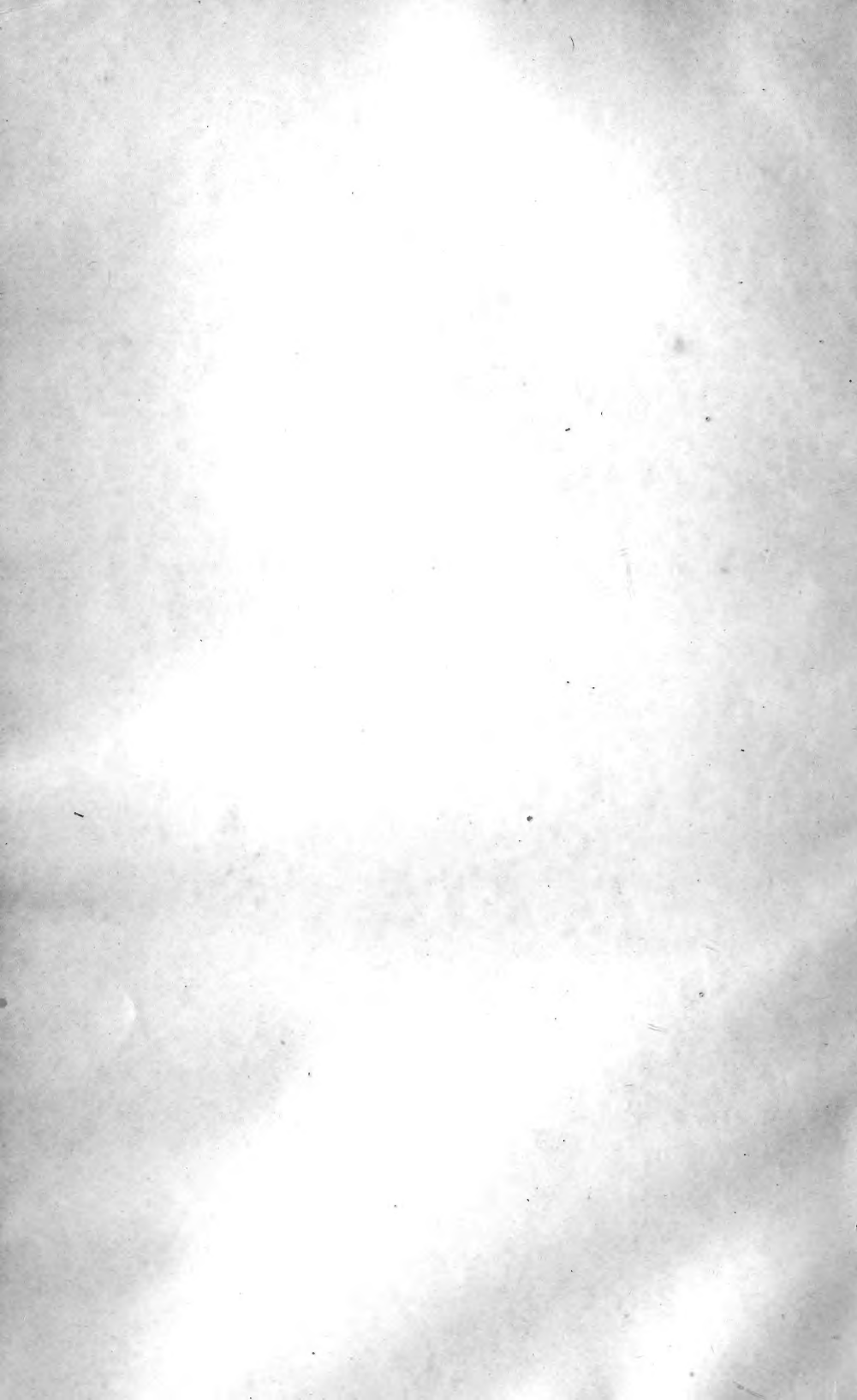














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Comparative Neurology

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Comparative Study of the Nervous System.

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THE

## JOURNAL OF COMPARATIVE NEUROLOGY.

## THE FINER STRUCTURE OF THE SPINAL GANGLION CELLS IN THE WHITE RAT.

By SHINKISHI HATAI.

*(From the Neurological Laboratory of the University of Chicago.)*

With Plate I.

The spinal ganglion of the white rat contains two very different kinds of ganglion cells. One is larger in size and less compact in the structure of the cytoplasm than the other (Figs. 1, 2, 3) and also stains lightly with eosin and erythrosin. This kind has been the most studied by previous investigators and its structure is comparatively well known. The second kind is very compact in the structure of the cytoplasm (Figs. 4, 5), stains deeply and is not so well known. The two kinds of ganglion cells have been found in all vertebrates in which the spinal ganglia have been carefully studied.

The present paper deals with the structure and significance of the small spinal ganglion cells.

The observations recorded may conveniently be presented in the following order:

- I. Technique.
- II. Measurements of the cells in the spinal ganglion.
- III. Internal structure of spinal ganglion cells.
- IV. Review of growth changes in the spinal ganglion.
- V. Summary.

## I. TECHNIQUE.

The white rat was used for the present work. Since the nerve cells are rapidly altered after death and also undergo changes in old age—as shown by HODGE<sup>1</sup>—care was taken to use material from animals freshly killed, and mature, but not senescent.

White rats, between 100 and 150 grams in body weight, were employed. Specimens of this weight are in the prime of life.

After being chloroformed, the animal was dissected and the ganglia removed. These were preserved separately in the following fluids. The preserving fluids, as well as staining agents, which have been recommended by previous authors are marked by the author's name above the formula. Fluids which are not named were devised by the writer:

1. *Carnoy's Fluid.*

Alcohol . . .	60 cc
Chloroform . . .	30 cc
Glacial acetic acid . . .	10 cc

2. *Ewing's Fluid.*

Mercuric chloride, sat. sol. in 5% Formalin.

3. *Graf's Fluid.*

Oxalic acid 80% . . .	4 vol.
Alcohol 95% . . .	3 vol.
Chromic acid 1% . . .	3 vol.

4. *Lenhossèk's Fluid.*

Corrosive sublimate, aq. sat. sol.

5. *Gilson's Fluid.*

Nitric acid of 46° strength . . .	78 cc
(This would be sp. gr. 1.456 or 80% nearly.)	
Glacial acetic acid . . .	22 cc
Corrosive sublimate, aq. sat. sol. . .	50 cc
60% alcohol . . .	500 cc
Distilled water . . .	440 cc

<sup>1</sup> HODGE—Changes in ganglion cells from birth to senile death. Observation on man and honey bees. *Journ. Physiology*, Vol. 17, '94.

*Fluids devised by the author.*

6.	Corrosive sublimate, Sat. sol. in formalin	30 cc
	Glacial acetic acid . . . . .	50 cc
	Normal salt solution . . . . .	15 cc
7.	Picric acid, sat. sol. in 10% formalin . . . . .	60 cc
	Glacial acetic acid . . . . .	20 cc
	Corrosive sublimate . . . . .	20 cc

In the above tables, the fluids which were recommended by the previous authors were used to preserve the materials according to the directions given. The other fluids which were new were employed in the following manner:

The tissue should remain in these fluids for 6 to 12 hours, according to the size of the piece. Generally thin pieces give more satisfactory results. After fixing, the tissue should be transferred to running water where it should remain 4 to 5 hours. Then it should be transferred to weak alcohol, about 30%. The further procedure is the same as for ordinary paraffin embedding.

As staining agents, all of the following were used on each piece of tissue:

1. Toluidin blue, aq. sat. sol.
2. Thionin, aq. sat. sol.
3. NISSL's fluid—as follows;  
Methylene blue (powder) (methylene B. pat.) 1.3 grms.  
White castile soap (Venice soap) . . . . . 0.7 grms.  
Distilled water . . . . . 332. cc.

For counter-staining:

1. Erythrosin 1% in 95% alcohol.
2. Eosin 1% in 80% alcohol.

As the clearing agents:

1. Xylol.
2. Cedar oil.

A comparison of sections prepared by the methods named above gave the following results. In each case, NISSL's stainable substance and the non-stainable substance came out very beautifully. The materials fixed with GILSON's fluid show greater shrinkage than those prepared by the other fluids. GRAF's fluid

has a weak penetrating power. CARNOY'S mixture gives very satisfactory results. This is a very simple but most safe fluid for general use. The author's own mixture gave quite as satisfactory results as CARNOY'S. Especially for the study of differences between the axone and dendrites to be elsewhere described, the author's fluid is preferable to any of the other fluids. In this fluid, the neurosomes of the axis cylinder stain very deeply but the neurosomes of the dendrites stain only lightly. The cell-bodies keep quite a good shape and never swell, as in the case of CARNOY'S fluid.

But the author believes with EWING<sup>1</sup> who studied ganglion cells in the human nervous system, that "more important than the choice of any particular fixative is the care in handling the tissue, and the exclusive dependence upon thin pieces of tissue, 1 to 2 mm., thick, which can be rapidly penetrated by all agents."

For staining, the author most often used thionin and toluidin blue, but a methylene blue was occasionally used. Good results were obtained from each of the staining fluids.

A counter-staining fluid was always used in the present work. For this purpose, erythrosin and eosin were tried and erythrosin gave the more satisfactory results.

## II. MEASUREMENTS OF THE CELLS IN THE SPINAL GANGLION.

Briefly, the spinal ganglion cells in the white rat form two groups distinguished, both by their chemical affinities and structural form, as has already been mentioned. The general form of the cell in section is somewhat oblong, this shape, however, is variable, and some of the cells are quite circular in outline. For the most part, the smaller cells which are surrounded by thick connective tissue or compressed among larger ganglion cell-bodies show triangular, polygonal or very rarely a spindle form. Very probably these irregular shapes result from the action of the preserving fluids.

The size of the cells in the cervical spinal ganglia (ganglia

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<sup>1</sup> EWING, J —Studies on Ganglion Cells, *Arch. of Neurol. and Psychopathology*, Vol. I, No. 3, '98.



from cervical enlargement) is quite variable ranging from  $55 \times 46 \mu$  to  $19 \times 17 \mu$  in diameter. The following table shows the size of the cell-body and its nucleus respectively:

TABLE I—Showing the size of the spinal ganglion cells in the cervical ganglia of the adult white rat.

Series A			
Cell-body	Nucleus	Cell-body	Nucleus
$51 \times 50$	$19 \times 15$	$56 \times 40$	$18 \times 15$
$60 \times 48$	$15 \times 15$	$58 \times 45$	$18 \times 16$
$56 \times 47$	$17 \times 15$	$59 \times 50$	$18 \times 15$
$55 \times 35$	$19 \times 15$	$55 \times 50$	$16 \times 16$
$50 \times 50$	$20 \times 15$	$50 \times 45$	$19 \times 15$
Average size . . .		$55 \times 46$	$18 \times 15$
Series a			
$34 \times 31$	$14 \times 14$	$36 \times 33$	$16 \times 15$
$39 \times 28$	$15 \times 13$	$30 \times 26$	$15 \times 12$
$44 \times 34$	$14 \times 16$	$42 \times 31$	$15 \times 14$
$40 \times 25$	$17 \times 15$	$40 \times 34$	$17 \times 15$
Average size . . .		$38 \times 25$	$15 \times 14$
Series B			
$30 \times 24$	$13 \times 11$	$25 \times 25$	$14 \times 13$
$26 \times 25$	$12 \times 12$	$25 \times 20$	$12 \times 11$
$25 \times 24$	$13 \times 12$		
Average size . . .		$26 \times 23$	$13 \times 12$
Series b			
$19 \times 15$	$10 \times 9$	$19 \times 15$	$10 \times 10$
$19 \times 19$	$10 \times 10$	$19 \times 15$	$11 \times 9$
$20 \times 19$	$11 \times 10$		
Average size . . .		$19 \times 17$	$10 \times 10$

*Series A.*—Measurements of largest cells, two from each section, taken from five successive sections, 6 to  $7 \mu$  thick.

*Series a.*—Measurements of cells next in size to the largest. Two cells in each case from the same sections used for Series A.

*Series B.*—Measurements of cells next in size to Series a. One cell in each case from the same section used for Series A, a.

*Series b.*—Measurements of smallest cells. One cell in each case from its same section used for Series A, a, B.

There is also a third group of cells which we shall designate Series C. This contains two kinds of cells in size, one being nearly the size of those in Series a, and the other the

same size as those in Series B, but never being found as large as those in Series A or as small as those in Series b.

This material, taken from the white rat with a body weight of 140 grams was fixed with formalin-acetic-sublimite mixture (6) and stained by toluidin blue and erythrosin.

As is shown in Table I the size of the cell-bodies is variable; the smallest have nearly the same size as in a young rat just after birth, but the largest ones attain nearly three times their diameter. These measurements of spinal ganglion cells in the white rat correspond to those obtained by other investigators in this laboratory. Between these extremes, many cells intermediate in size are noticeable. Before going on to discuss the peculiarities of these cells, it may be well to compare the diameters of the spinal ganglion cells in other vertebrates with those in the white rat.

BUEHLER<sup>1</sup> measured the spinal ganglion cells in several classes of vertebrates. He obtained the following results:

TABLE II—Showing the diameter in  $\mu$  of spinal ganglion cells in various vertebrates—after BUEHLER.

First column gives the average diameter.  
Second " " " diameter of the largest cells.  
Third " " " " " smallest cells.

Name	Average	Largest	Smallest
Fish ( <i>Leuciscus rutilus</i> ) 14 c m long	20	30	10
Frog	40-50	70-80	10-20
Lizard		25	20
Dove	30-40	50	12-20
Cat	50+	70-80	22
Rabbit	50+	70-80	16
Dog	50+	108	24
Man	45-67	120	20

He also noticed that the spinal ganglion contains a greater number of small than of large cells.

CAVAZANNI<sup>2</sup> also measured the diameters of spinal ganglion

<sup>1</sup> BUEHLER, A.—Untersuchungen über den Bau der Nervenzellen. *Würzburg*, '98.

<sup>2</sup> CAVAZANNI, E.—Sur les Ganglion Spinaux. *Arch. Ital. de Biologie*, T. xxviii.

cells in several kinds of mammals in adult and embryonal stages, but does not give separate measurements for the small and large cells.

From the observation of these two authors, it is known that the spinal ganglia of all vertebrate animals thus far examined contain two kinds of the cells. The question arises, whether all of these cells are functional or not, and, if functional what is indicated by this variation in size? To assist in forming an opinion on this point let us first describe the internal structure of these cells and make a comparison between their structural differences.

### III. INTERNAL STRUCTURE OF SPINAL GANGLION CELLS.

Different arrangements of the stainable substance in the spinal ganglion cells according to the different sizes of the cell-bodies have been noticed by several authors, and according to these arrangements, they have tried to classify the cells. Some of these classifications are as follows:

NISSL<sup>1</sup> found in spinal ganglion of rabbit, the different classes of cells which he has distinguished and recognizes the great differences in the size of the cell-body. He further notes a number of varieties of cells characterized by the size of the masses of stainable substance. Using this as a criterion he distinguishes (1) those in which the stainable substance consists entirely of large masses, (2) those in which it consists of very small masses, (3) those in which both large and small masses are present. In this case the two sizes of stainable masses can be present in equal numbers or either the smaller or the larger may be in excess. (4) Both large and small masses of stainable substance may be present with a peculiar arrangement of the masses of a given size thus imparting to the cell a characteristic appearance.

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<sup>1</sup> NISSL.—Ueber die sogenannten Granulæ der Nervenzellen. *Neurolog. Centralblatt*, '94, Nos. 19, 21, 22.

Ueber die Nomenclatur der Nervenzellenanatomie und ihre nächsten Ziehle. *Neurolog. Centralblatt*, '95, No. 23.

LUGARO<sup>1</sup> distinguishes in the dog five different varieties of the spinal ganglion cells.

I. Large clear cells with delicate, closely packed stainable masses which are distributed uniformly throughout the cell-body. Around the nucleus, the stainable masses are more closely packed. The nucleus is large, clear and is provided with a nucleolus. These cells appear to be numerous in spinal ganglion.

II. Clear, medium-sized cells with irregularly formed small and large stainable masses which are large at periphery. Even here we see that individual masses are not isolated but are united together by fine processes. The nucleus is clear and possesses a nucleolus. These cells are most numerous.

III. Small, dark cells with small numerous stainable masses. Larger masses lying in region of the nucleus. The ground substance becomes diffusely stained. The nucleus also stains diffusely and contains two or more nucleoli. These cells rank third in point of number.

IV. Small and medium sized clear cells with large stainable masses which are present in small numbers and connected with each other by processes. The nucleus frequently possesses more than one nucleolus. These cells are not numerous.

V. Large, clear cells with long drawn out masses which are continuous with one another and arrange themselves in concentric lines around the nucleus. These last cells present a laminated appearance like the cross section of an onion. These cells are least numerous.

LENHOSSEK<sup>2</sup> divided the spinal ganglion cells into the following three varieties :

The first variety consists of cells with a very pale ground substance only. These, which are the largest cells, have a dense ground substance and with less numerous and loosely arranged stainable masses, which are most dense around the nucleus.

<sup>1</sup> LUGARO, E.—Sulle alterazioni delle nervosi dei ganglia spinali. *Rev. di pathol. nerv. e ment.*, Firenze, Vol. V ('96) Nos. 8 and 12.

<sup>2</sup> LENHOSSEK—Ueber den Bau der Spinalganglienzellen des Menschen. *Arch. f. Psychiat. u. Nervenk.*, Berl., Bd. XXIX ('96-'97), S. 346-380.

To the second variety belongs a coarse granular cell (größscholligen Zellen), the appearance of which depends on the appearance of the stainable substance, and most of the cells belong to this variety. These cells are of medium size, but sometimes small and rarely very large.

The third variety contains the spinal ganglion cells which have a peculiar internal structure. These cells stain darkly because of the density of the ground substance.

Cox<sup>1</sup> describes in the rabbit two main varieties of spinal ganglion cells:

One variety contains larger or smaller irregular masses of stainable substance, which do not show a distinct concentric arrangement. The cells of this variety may be either large or small.

The other variety contains large, irregular masses of stainable substance arranged concentrically.

From these citations it is clear that the above authors classified the spinal ganglion cells in accordance with the three following characters: (1) Size of the cell body; (2) The arrangement of stainable substance; (3) Chemical reactions of the ground substance. Using the characters just named we shall in this paper make still another classification which will be presented in detail below.

The smaller cells in the white rat measure only 25 to 18  $\mu$  in diameters, and the nucleus 12 to 10  $\mu$  in diameter. Such small cells are more numerous than the larger cells and stain more deeply. One group of these smaller cells stains so deeply with erythrosin and eosin that one can easily distinguish them from the larger ones. A careful study of these smaller cells which stain next deeply shows that the stainable substance is thickly massed around the peripheral portion of the cell. Near the nucleus, the stainable substance is very scanty. The stainable masses are of large size only at the extreme periphery of the cell and the remaining part is filled up with fine powdered

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<sup>1</sup> Cox, W, H.—Der feinere Bau der Spinal Ganglienzelle des Kaninchens. *Anatomische Hefte*, Abth. 1, Bd. 10, '98.

granules. No "clear zone," which is present in the larger cells between the cytoplasm and the nucleus, is visible. For this reason the outline of the nucleus is less sharp and the cell-body appears somewhat structureless or homogeneous.

Besides these cells, still another variety of smaller cells is observable. The cell-body stains nearly as deeply as the small cells described in the previous paragraph. No clear zone is visible around the nucleus. The arrangement of the stainable substance resembles very much that of the larger cells. The masses of stainable substance are of large size and distributed through out the cell-body without showing any constant or fixed arrangement. Small masses of stainable substance are also noticeable throughout the cell-body. No such phenomenon as the accumulation of the stainable substance in large masses or the forming of the large sized stainable masses only at periphery is visible, as in the case of many other cells both large and small. The ground substance is dense. LENHOSSEK<sup>1</sup> called attention to this density of the ground substance in the following way :

"Die kleineren Zellen unterscheiden sich nun von den grösseren nicht nur durch ihre geringeren Dimensionen, sondern in sehr auffallender Weise auch durch ihre besonderes färberisches Verhalten. Im Allgemeinen kann man sagen, je kleiner eine Zelle ist, desto intensiver verbindet sie sich mit den meisten Farbstoffen, namentlich mit denjenigen, die das Protoplasma färben. Die Erscheinung ist hier nicht in der Gegenwart von besonderen Körnerbildungen oder dergl. begründet, obgleich die kleineren Elemente in ihren Randschichten relativ gröbere Plasmaschollen beherbergen als die grossen, sondern hängt, wie ich mich diesmal mit Bestimmtheit überzeugt habe, in erster Reihe mit einer dichteren Beschaffenheit der Grundsubstanz des Protoplasma zusammen."

We can fully corroborate this observation of LENHOSSEK, but the writer noticed in many cases that the NISSL's stainable

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<sup>1</sup> LENHOSSEK—Centrosom und Sphäre in den Spinal Ganglienzellen des Frosches. *Arch. f. mikr. Anat. und Entwicklungsgeschichte*. Bd. XLVI, H. 2, '95.

substance in the powder form is also quite abundant in these cells. This contributes to the dark appearance of the cell-body. These cells just described are generally larger than those mentioned in the first paragraph. In the former case, the cell-body looks structureless. But the writer's observation shows, this is not homogeneous or structureless in the strict sense of the word as is indicated by the statement that this cells stain somewhat darkly because of density of the ground substance. A well preserved and satisfactorily stained preparation shows very clearly that the cytoplasm is filled up very densely with a peculiar substance named by HELD<sup>1</sup> the "neurosomes" which are stainable only by acid dyes. There are so many of these neurosomes that one can hardly distinguish one individual from another and the cytoplasm appears a continuous reddish mass. The small cells (in Series C) are in the same condition, having great numbers of neurosomes. From this is quite clear that the chromophilic cells, as named by NISSL, are peculiar in the arrangement of the neurosomes.

Another interesting point concerning the small cells is that in every case the cell-bodies shrink a little more than those of larger cells. My own mixture for preservation (6) gives the cells in a nearly normal size and no spaces appear around the cell-body in the case of the larger cells. But around the small cells such spaces are to be seen. This shrinkage has been interpreted as a pathological change but one can hardly believe that there are so many pathological cells in the normal spinal ganglion. It should be remembered that the spinal ganglion contains a greater number of the small cells than of those larger in size. We will explain later why the small cells tend to shrink.

Let us first compare these small and large cells as to the arrangement of the masses of stainable substance in them. These masses in the larger cells are arranged in a more complex

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<sup>1</sup> HELD, H.—Beiträge zur Structur der Nervenzellen und ihrer Fortsätze. Erste Abhandlung. *Arch. für Anatomie und Entwicklungsg.*, Anat. Abth. '95

way than in the smaller cells. The writer has distinguished three types of arrangement in the larger cells.

One type presents coarse and large masses which exist throughout the cell-body without showing any fixed arrangement. Clear spaces around the nucleus and at the extreme periphery of the cell-body are very distinctly visible (Fig. 1). Besides the coarse masses, minute powder-like granules are visible (see Fig. 2). This type of cell is very abundant.

A second type of these cells has large and coarse masses only at the periphery (Fig. 2), but the remaining part shows much smaller masses. The arrangement of masses of stainable substance is faintly concentric. The clear zones about the nucleus and at the periphery are visible. These cells are also very numerous in the spinal ganglion.

In the last type of cells, the stainable substance exhibits a beautiful concentric arrangement around the nucleus (Fig. 3). The stainable masses are rather large in size, although in some cases they may be small, and as in the first type the large stainable masses are distributed throughout the cell-body. The stainable masses show an elongated spindle form. As LUGARO'S picture shows, this type of cell suggests the cross section of an onion. When the level of section passes through the more peripheral portion of the cell-body, the stainable masses show a somewhat parallel arrangement, and sometimes they are continuous, making a strong heavy line. The clear zones are brilliant. This type of cells is not so abundant. The writer has classed these three types of the cells as larger cells (Table I, Series A and a).

Another type of cell was observed by the writer, the measurements for which are given in Table I, Series C. Curiously enough, this type of the cell body stands between the larger and smaller cells as "intermediate" in structure. The structure of the cell-body is as follows: The masses of stainable substance distribute themselves throughout the cell-body in concentric or irregular layers. The size of the cell-bodies is variable; the larger cells measuring  $38 \times 24 \mu$  and the smaller  $26 \times 21 \mu$  in diameter. The most important and interesting



point is that the cell-body stains deeply with eosin or erythrosin as in the case of smaller cells. The clear zones are less differentiated than those of the larger cells. The cell-bodies do not shrink so much as those of smaller cells and sometimes do not show even a slight trace of shrinkage. For a better comparison we will summarize the various descriptions of the spinal ganglion cells which have just been given.

### *I. Larger Cells.*

A. Table I, Series A and a, Fig. 1. The cells with large, coarse stainable masses which lie throughout the cell-body without showing a regular or constant arrangement.

B. Table I, Series A and a, Fig. 2. The cells with large, coarse stainable masses only at the periphery. Smaller masses fill up the remaining part.

C. Table I, Series A and a, Fig. 3. The cells with large, coarse stainable masses which lie throughout the cell-body, showing a regular, concentric arrangement.

### *II. Smaller Cells.*

A. Table I, Series B and b, Fig. 4. The cell-body of small size, stainable masses accumulated at the periphery of the cell. The cell-body stains deeply in eosin and erythrosin. After fixing it has a tendency to shrink markedly.

B. Table I, Series B and b, Fig. 5. The cell-body is of small size. Stainable masses are large and distributed throughout the cell-body. The cell body stains very deeply as in the former case. There is no regular arrangement of the stainable substance. After fixing it has a tendency to shrink markedly.

### *III. Intermediate Cells.*

A. Series C. The cell-body small or large size. The stainable masses are large and coarse and are distributed throughout the cell-body with or without showing a concentric arrangement. The cell-body stains deeply as in the case of smaller cells. These cells have a tendency to shrink slightly.

B. Series C. The cell-body is of small or large size. The

stainable masses are large at the periphery as in Fig. 2. The remaining part of the cell-body is filled up with small stainable masses. The arrangement of the masses is not regular. The cell-body stains deeply and has a tendency to shrink slightly.

This large number of varieties among the spinal ganglion cells calls for an explanation.

It seems to me very probable that the smaller cells, which were regarded as in a pathological condition or as artifacts (chromophilic cell) by some of the previous investigators<sup>1</sup> are in many cases the growing stages of the normal cells.

To support this view let us consider the evidences of growth in the spinal ganglion as determined by other investigators.

#### IV. REVIEW OF GROWTH CHANGES IN THE SPINAL GANGLION.

HODGE<sup>1</sup> counted in the frog the number of fibers in the posterior root and the number of the cells in the spinal ganglia of several nerves. From these observations he obtained the following results:

TABLE III.—Showing the number of fibers and cells in the afferent spinal nerves of a Frog (probably Bull-frog). Weight not given but probably 150 grams in body-weight—(after HODGE).

No. fibers in dorsal root		No. of cells in ganglion.	Excess of cells	Ratio of one fiber to cells.
Seventh nerve (Right side)	1128	2767	1639	1:2.45
Eighth nerve (Left side)	1811	5416	3605	1:2.94
Seventh nerve (Left side)	1364	4456	3104	1:3.26
T's count	1340			

From the above table, we find that one afferent fiber of

<sup>1</sup> The word chromophile was first used by FLESCHE to describe the cells which stain diffusely; later NISSL applied the term to the cells in which the stainable substance appears to be evenly diffused throughout the cell-body. This kind of the cells was considered by NISSL as pathological or an artifact (NISSL, *Allg. Zeschr. f. Psychiat.* etc., Berl. ('96), Bd. iii, S. 8).

<sup>1</sup> HODGE, C. F.—Some effects of electrically stimulating ganglion cells. *Amer. Journ. of Psychology*, Vol. II, '88.

the frog corresponds in these cases to from 2.45 to 3.26 of the spinal ganglion cells.

BUEHLER<sup>1</sup> obtained the following results from the examination of ninth spinal nerve of the frog (*Rana esculenta*). He found in dorsal root 680 fibers and in the spinal ganglion about 3500 cells giving a ratio of 1 to 5, while according to LEWIN<sup>2</sup> in the 32nd spinal nerve of the rabbit there were found only 3173 posterior root fibers to correspond to the 20361 cells of the spinal ganglion; a ratio of 1:6.4.

BIRGE<sup>3</sup> was able to show in the frog, first that the number of fibers found in the dorsal and the ventral spinal nerve roots increased as the frog increased in size, and second that in both the IIInd and IXth nerves there was an excess of fibers in the trunk over and above the sum of the fibers in the two roots. This excess amounted to 16% in the case of the IIInd nerve and 14%, for the IXth.

HARDESTY'S<sup>4</sup> studies on the spinal nerves of the frog gave us some important results. He summarized his observations as follows:

"1. The number of fibers in the ventral roots decreases from the spinal cord toward the spinal ganglion.

"2. The number of fibers in the dorsal roots decreases from the spinal ganglion toward the spinal cord.

"4. The section of the nerve trunk immediately distal to the spinal ganglion (dorsal branches excluded) contains a

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<sup>1</sup> BUEHLER, A.—Untersuchungen über den Bau der Nervenzellen. *Verhandlungen der Physik.-med. Gesellschaft zu Würzburg*. N. F. Bd. 31, p. 285, '98.

<sup>2</sup> LEWIN, VON TH.—Ueber die Zahlen der Nervenfasern und Ganglienzellen in den Spinal Ganglien des Kaninchens. *Centralbl. für Physiologie*, '96, Heft 15 und 16.

<sup>3</sup> BIRGE, E. A.—Die Zahl der Nervenfasern und der motorischen Ganglienzellen im Rückenmark des Frosches. *Archiv für Anatomie und Physiologie. Physiologische Abtheilung*. H. 5 und 6, 1882.

<sup>4</sup> HARDESTY, I.—The Number and Arrangement of the Fibers forming the Spinal Nerves of the Frog (*Rana virescens*). *J. of Comp. Neurol.*, Vol. IX, No. 2, '99.

greater number of fibers than are found in a section of the trunk further distal.

"5. The decrease in the number occurs among the smaller fibers of the nerve.

"6. The general explanation of these relations is found in the fact that the fibers arising from the spinal ganglion grow, on the one hand, toward the spinal cord by way of the dorsal root and, on the other hand, toward the periphery by way of the nerve trunk; and, that the fibers of the ventral root grow from the spinal cord towards the periphery.

"7. In frogs of increasing weight, the fibers of the dorsal root increase in number more rapidly than do those of the ventral root."

From the investigations of the above named authors it is evident that the number of cells in the spinal ganglia is greater than the number of fibers in the corresponding dorsal nerve root. This is true for the mammal represented by the rabbit, as well as for the frog. Further, HARDESTY has shown in the case of frog that fibers in the dorsal and ventral nerve roots, as well as in the nerve trunk, are distributed in different levels as though nerve fibers were continuously growing out from ventral horn cells on one hand and the spinal ganglion cells on the other, and he interprets his results as indicating growth. In mammals, however, DALE<sup>1</sup> was unable to find this indication of growth in the mature cat. If this arrangement in the cat should prove to be constant, the difference between the cat and the frog might be explained by long continued growth changes in the frog as compared with very rapid enlargement of the cat to a fixed size. Besides the excess of the cell-bodies in the spinal ganglion of both frog and rabbit and evidence of the growth changes in the frog, we have our own observation that the smallest and smaller ganglion cell-bodies are in the white rat most numerous and LENHOSSEK reports the same for the dog, and BUEHLER for the frog.

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<sup>1</sup> DALE—On some Numerical Comparisons of the Centripetal and Centrifugal Medullated Nerve Fibers arising in the Spinal Ganglia of the Mammal. *Journ. of Physiology* (FOSTER), Vol. XXV, No. 3, 1900.

HARDESTY has shown that in the frog it is the very small nerve fibers which represent those which are growing, while observations based on the GOLGI method show that in the spinal ganglia as a rule the size of the cell process is proportional to the size of cell-body, a larger cell-body sending off a larger process.

DR. DONALDSON<sup>1</sup> obtained the following results from his observations which were made upon growing nerve cells in the white rat, as they appear between birth and maturity. He says that "in the growing spinal ganglion of the lumbar nerves, the increase in volume of the largest ganglion cell-bodies was shown to be very closely correlated with the increase in the area of a cross section of the nerve fiber growing out of these cell-bodies." The following table shows the relations just mentioned more in detail:

TABLE IV.—The relative volumes of the cell bodies and areas of the cross section of the nerve fibers of the growing white rat of different weights—After DONALDSON.

Body weight grams	Volumes of gan- glion cells	Areas axis	Areas axis and sheath
4.7	1.0	1.0	1.0
10.4	1.6	1.4	2.8
25.7	4.9	4.6	9.3
68.5	11.2	12.2	24.0
159.0	15.0	14.4	29.7

From the above table, it is evident that the larger sized cell-body sends off larger sized processes, and smaller cells the smaller processes.

No author has ever counted the smaller and larger ganglion cells separately. HARDESTY<sup>2</sup> gave the table showing separately the number of small and large fibers forming the dorsal and ventral roots. This gives a general idea concerning the numerical relations between small and large cells in the frog.

<sup>1</sup> DONALDSON, H. H.—The Functional Significance of the Size and Shape of the Neurone. *Journal of Mental and Nervous Disease*, Oct., 1900.

<sup>2</sup> HARDESTY, I.—Loc. cit.

TABLE V—Showing the small and large fibers separately in dorsal and ventral regions of spinal nerve of Frog (*Rana virescens*)—After HARDESTY.

In the following table, Sec. 1 and Sec. 3, mean the two different levels of sections. Small fibers are those 5  $\mu$  or less in diameter

Nerve	Fibers	Sec. 1	Sec. 3	Dif.
III N.	{ Dors.	{ Small 155	164	9
		{ Large 162	165	3
	{ Vent.	{ Small 306	289	17
		{ Large 91	90	1
V N.	{ Dors.	{ Small 193	203	10
		{ Large 95	96	1
	{ Vent.	{ Small 45	39	6
		{ Large 88	88	0
VII N.	{ Vent.	{ Small 107	95	12 <sup>3</sup>
		{ Large 284	282	2

As the above table shows, the small fibers in some nerves are more numerous than the large fibers. It seems very probable that some of the small cells are still in an immature condition and have not yet sent off an axone. If this is true, then there must be a greater number of these small cells than is represented by small fibers in the nerve root.

From this numerical relation, it seems to me that small cells are in an immature or growing stage. This can be shown to be true in another way. The writer gave a hint in the preceding pages that the small cells show a tendency to shrink readily. We know that a cell-body which contains much water is harder to preserve in a normal state than the cells with less water. The cells with more water show more shrinkage. It is already known that the animal body contains when young comparatively a greater quantity of water than the mature animals.

I am allowed to quote from some unpublished observations of DR. DONALDSON on the white rat at birth and at maturity which show the following percentages of water in the central nervous system.

TABLE VI—Percentage of water in white rat at different ages—After DONALDSON.

Age	Brain	Spinal Cord
Birth	87%	85%
Maturity	78%	72%

This decrease occurs gradually, and after the animal reaches its mature condition remains nearly constant. The high percentage of water in the whole nervous system indicates that the nerve cells probably contain much water; that is to say, it appears from this justifiable to conclude that nerve cells in the growing condition contain the larger quantity of water and since the cells with the larger quantity of water are most readily shrunk, the phenomena of shrinkage in the small cells does not signify a pathological condition, but shows that the cell body is physiologically immature, that is contains the higher percentage of water which is necessary for its growth.

Let us compare the structure of the small cells of the adult animal with the cells of a young rat. The difference in cell-size in the spinal ganglion appears during uterine life. In a white rat weighing 4.52 grams differences in size are already quite clear. The large cells attain the diameter of about  $25\ \mu$  and the nucleus about  $12\ \mu$ . On the other hand, the small cells only attain  $14\ \mu$  in the diameter of the cell-body and their nucleus  $8.5\ \mu$ . In this stage, the small cells have a comparatively large nucleus and little cytoplasm. The stainable substance is diffused through the cytoplasm in this early stage. In the white rat of 10.84 grams body-weight, the large cells attain  $35\ \mu$  in the mean diameter and the nucleus  $16\ \mu$ . The small cells in this stage measure  $14.1\ \mu$  in the mean diameter of the cell-body and  $9.7\ \mu$  in the mean diameter of the nucleus. In the rat weighing 10.84 grams the outlines of the large cells are sharply bounded and the cell-body stains strongly with methylene blue. The small cells, however, not only maintain nearly same size as at birth but also the cell-body shows the same appearance as in the case of the new-born rat.

In the next stage, namely in the rats of 25.1 grams in the body-weight, the large cells develop remarkably, attaining  $39\ \mu$  in the mean diameter of the cell-body and  $13\ \mu$  in the mean diameter of the nucleus. The small cells, on the other hand,

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<sup>1</sup> The writer observed in the embryo of *Amia calva* in which difference already takes place when it is 6 mm. long.

develop hardly so fast, attaining  $15\ \mu$  in the mean diameter of the cell-body and  $10\ \mu$  in the mean diameter in the nucleus. In the later stages, as in the previous case, only the large cell grow rapidly while the small cells remain nearly the same size.

Finally, in the rats at maturity, the large cell-bodies attain  $50\ \mu$  in the mean diameter while small cells are only  $18\ \mu$  in the mean diameter.

On comparing the cell-size of the matured cells with those of animals just born, it appears that the large cells in the adult white rat attain about twice the diameter of those of a white rat just born. On the other hand, the small cells in the adult rat maintain nearly the same size as those in the new born rat, showing the difference of about  $4\ \mu$  in mean diameter. These relations are presented in the following table :

TABLE VII—The large and small spinal ganglion cells in cervical ganglia of the white rat of different weights.

Weight	Large		Small	
	Cell-body	Nucleus	Cell-body	Nucleus
4.52	$25\ \mu$	$12\ \mu$	$14\ \mu$	$8.5\ \mu$
10.84	35	16	14.1	9.7
25.1	39	16	15	10.
68.8	37	17	14.4	10.
157.	50	17	18	10.

From the above observations, the following conclusion is reached :

- (1) The differentiation in the size of the cell-bodies appears in the rat in early foetal life.
- (2) The diameter of small cells in an adult white rat is only slightly greater than that at birth.
- (3) The internal structure of the small cells in an adult white rat shows the same appearance as that at birth.
- (4) The nucleus remains relatively large: a striking character of immature nerve-cells.

BUEHLER<sup>1</sup> made the following suggestions concerning the

<sup>1</sup> BUEHLER, A.—Loc. cit., p.16.



small cells: "Es kommt, wie ich mich bei Frosch und Kröte und auch beim Kaninchen überzeugen konnte, physiologischer Weise zum Untergang speciell der grossen Spinalganglienzellen. Die Degeneration verläuft in verschiedenen Formen und allem Anschein nach wenig rapid. Man sieht in einem Spinalganglion des Frosches ca. 20—25 untergehende Zellen, beim Kaninchen relativ noch viel weniger. Die verloren gegangenen Zellen müssen ersetzt werden, und dies geschieht wahrscheinlich dadurch, das eine der Kleinen durch Wachstum ihre Stelle einnimmt. Da nach dem frühesten Jugendstadium eine Vermehrung von Nervenzellen nicht mehr vorkommt, muss das Spinalganglion, um für die Zeit des Lebens functionsfähig bleiben zu können, in der Anlage genügendes Ersatzmaterial in Gestalt von Reservezellen mitbekommen. Genauere Untersuchungen hierüber zu machen, bin ich indess noch nicht in der Lage gewesen."

From this we see that BUEHLER considers that some of the largest cells degenerate during the life of the animal and that the place of the degenerating cells is taken by some of the small cells which have remained immature and ready to develop as the occasion demands.

LENHOSSEK<sup>1</sup> regards these small cells as immature or "Jugendlich." He most often found the centrosome in the cells of this type.

DOGIEL<sup>2</sup> studied the spinal ganglion cells with methylene blue which was injected into the living animal (dog, cat, rabbit and guinea pig). In these preparations he noticed two kinds of the spinal ganglion cells which he designated as I type and II type, respectively. To these types he gives the following characters:

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<sup>1</sup> LENHOSSEK—Centrosom und Sphäre in den Spinalganglienzellen des Frosches. *M. Schultze's Arch.*, XLVI, p. 345, '95.

<sup>2</sup> DOGIEL, A. S.—Der Bau der Spinalganglien bei den Säugethieren. *Anat. Anz.*, '96, Bd. XII.

DOGIEL—Zür Frage über den feineren Bau der Spinalganglien und deren Zellen bei Säugethieren. *Internat. Monatschr. für Anat. und Physiologie*, Bd. XIV, '97, Heft, 4 und 5.

I type of Cells—This form of cell is represented by two varieties; one measures  $77-175\ \mu$ <sup>1</sup> in its long diameter, while the breadth is  $43-86\ \mu$ ; the other measures  $21-30\ \mu$  in its long diameter and the breadth is  $12-25\ \mu$ . The latter appears by the method in smaller numbers. This variety of cell receives the axone from II type of cells. The fiber of this I type cell divides into two branches, forming the "T" shaped fiber. These cells are those ordinarily called the ganglion cells.

II type of Cells—The axone of such a cell breaks up within the ganglion into a large number of branches. The branches lose their myelin sheaths and terminate about the cells of I type, forming a pericellular basket. The second type receives the termination of axone from sympathetic ganglion cells. The cell-body measures  $43-132\ \mu$  in long diameter, while its breadth is only  $30-55\ \mu$ .

Slight differences occur, however, as regards the morphology of these two varieties under Type I. The fiber of the larger cells is sheathed by medullary substance or myelin in all cases, while the fiber of the smaller cells is destitute of myelin except in a few cases. When the fiber is destitute of the myelin sheath, the axone shows a varicose appearance. These observations by DOGIEL bear very directly on the suggestion of the writer that these small ganglion cells are not pathological, as has been maintained, but immature. For DOGIEL here shows (1) that some of the small cells give off axones of the typical spinal ganglion forms; (2) that the axone is often unmyelinated, itself sign an immaturity, and (3) finally that the number of these cells from which no axone is to be traced is large and hence these are not to be considered as functional at this stage of development.

From these several observations, the writer concludes that the small cells of the spinal ganglion are in a growing state or in a more or less permanently immature condition. The grow-

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<sup>1</sup> It is to be noted that the measurements of the spinal ganglion cells made by DOGIEL do not greatly exceed those given in Table II when the mean of the several diameters is taken.

ing fibers which are found in an adult frog might, therefore, very well be formed by the axones of these latent cell-bodies.

We have ventured to classify the spinal ganglion cells in a few groups but noticed that each group contains many varieties of the cells which were at first puzzling. These varieties appear to be the transitional stage.

If the spinal ganglion cells, are classified according to the measurements of size, then would follow:

I. Large cells (Series A and a); cells in completely mature stages.

II. Intermediate cells (equal in size to those in Series a and B); cells in both mature and immature stages.

III. Small cells (Series B and b); cells in immature stages.

## VI. SUMMARY.

I. The spinal ganglion of the white rat contains two varieties of the cells; one variety is larger in size and stains lightly with eosin and erythrosin; another variety cells is smaller in size and stains deeply with eosin or erythrosin.

II. Besides the above two varieties, the spinal ganglion of the white rat contains one more distinct variety of the cells. This stands as "intermediate" in its structure and size between the two former varieties.

III. The small spinal ganglion cells which were described as chromophilic cells are considered by the writer as in an immature or growing condition, and not as pathological nor as artefacts as has been maintained by some of the previous authors.

IV. When the spinal ganglion cells of the white rat are classified according to size, into large, intermediate and small cells, these three groups are also found to be regularly graded in their internal structure.

## DESCRIPTION OF THE FIGURES.

## PLATE I.

The following figures were made by camera with same magnifying powers using the ocular (No. 1) and the objective (1-12) of Bausch and Lomb.

*Fig. 1.* Large spinal ganglion cells from ganglia of the cervical enlargement of the white rat.

*Fig. 2.* Do Do

*Fig. 3.* Do Do

*Fig. 4.* Small spinal ganglion cells from ganglia of the cervical enlargement of the white rat.

*Fig. 5.* Do Do

# ON THE PRESENCE OF THE CENTROSOME IN CERTAIN NERVE CELLS OF THE WHITE RAT.

By SHINKISHI HATAI.

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With Plate II.

In the present paper, the writer describes the appearance of the centrosome in certain nerve cells of the white rat. The description is presented under the following heads:

I. Materials used and technique employed in this investigation.

II. The different groups of the cells in which the centrosome was discovered.

III. The morphology of the centrosome.

IV. Historical review of the centrosome in nerve cells.

V. Summary.

VI. Illustrations of the centrosome in the nerve cells of the white rat.

## I. MATERIALS USED AND TECHNIQUE EMPLOYED IN THIS INVESTIGATION.

The materials used for the present investigation were taken from new-born white rats having a body-weight of 4.6-6.0 grams and adult white rats having a body-weight of 150 grams. Besides these animals, a young mouse (weight unknown) was used for comparison.

As a killing fluid, the writer's<sup>1</sup> new mixture (sublimate-acetic formalin mixture) was most frequently used. Besides this,

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<sup>1</sup> HATAI, S.—Finer structure of the spinal ganglion cells in the white rat. *Journ. of Comp. Neurology*, Vol. XI, No. 1, 1901.

GILSON's acetic-nitric-alcohol mixture and CARNOY's acetic-chloroform-alcohol mixture were also used with advantage. VON LENHOSSÈK ('95) who first investigated the centrosome in the spinal ganglion cells of the frog used an aqueous solution of corrosive sublimate. DEHLER ('95) stated that osmic preparations give unsatisfactory results; nevertheless LEWIS ('96) has obtained very beautiful results from her osmic preparations of a certain annelid. HOLMGREN ('99) employed the fluid recommended by CARNOY. NELIS ('00), who studied mammalian nerve cells under pathological conditions for the purpose of demonstrating the centrosome, employed GILSON's fluid. The present writer obtained satisfactory results from all these fluids but most frequently employed his own mixture, not because it is necessarily superior to the others, but because the writer was most familiar with its action.

As staining agents, toluidin blue and thionin were used. The further procedure was the same as that given in the paper on the structure of the spinal ganglion cells.<sup>1</sup>

## II. THE DIFFERENT CLASSES OF THE CELLS IN WHICH CENTROSOMES WERE DISCOVERED.

Before going on to describe the structure of the centrosome, the different classes of the nerve cells in which the present writer has found the centrosome may be here enumerated.

Two young white rats, having body weights of 4.6 and 6 grams respectively, and three adult white rats, each having a body weight of approximately 150 grams were used. The young rats were new-born. The regions examined from these animals were the cortex of the cerebrum, cerebellar cortex, corpus dentatum, motor cells in the ventral horn of the spinal cord and the spinal ganglia. The sections were cut  $6\mu$  in thickness. Three or four slides were made from each of the regions just mentioned. Every section on each slide was carefully examined. In this study it was observed that most of the nerve cells of young white rats possess a centrosome and a well

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<sup>1</sup> loc. cit.

marked sphere. In the adult white rats, however, the nerve cells which contain these structures are by no means so abundant.

The following table shows the localities in which the centrosome was observed :

TABLE I. Showing the groups of the cells of the white rat in which centrosome has been found.

Age	Largest cells in cerebral cortex	Purkinje's cells	Nucleus of corpus dentatum	Motor cells in ventral horn spinal cord	Cells in spinal ganglion
Adult	present	present	o	o	present
Young	present	present	present	present	present

It is interesting to find that the centrosome is so widely distributed through the central nervous system, of the young as well as the adult white rat, while some authors—viz., NELIS, FLEMMING—claim that the centrosome can not be found in the normal nerve cells of the higher mammalia. In adult animals, the writer could not find the centrosome either in the nucleus of the corpus dentatum or in the cells in the ventral horn of spinal cord, although it was clearly to be demonstrated in these localities in the case of young animals. It is a reasonable supposition, however, that the invisibility of the centrosome in these two regions in the adult white rat is due to the large quantities of the stainable substance which fills up these nerve cells and thus obscures the presence of the centrosome. The writer noticed, very often, structures similar to the centrosome in both these regions; but was unable to determine its structure with certainty because not only the clear space but also the radial arrangements of cytoplasm, which is most characteristic for the centrosome, were obscured by the presence of many small granules of a uniform size.

The writer believes, however, that more improved methods both in preserving as well as staining would overcome these difficulties and reveal the centrosome in these localities also.

## III. THE MORPHOLOGY OF THE CENTROSOME.

As is shown in the illustrations, the centrosome as well as the sphere<sup>1</sup> in PURKINJE cells and in the pyramidal cortical cells, lie, as a rule, at the base of a main dendrite near the nucleus (Figs. 2, 3, and 5-10). On the other hand, the centrosome and the sphere in the spinal ganglion cells lie, as a rule, on the side of the nucleus towards the axone hillock (Figs. 1, 11).

The centrosphere is somewhat circular in cross section with a less quantity of protoplasm. This gives the clear and transparent appearance to the centrosphere. A coarse granular layer of the protoplasm surrounds the centrosphere, which layer VON LENHOSSÈK termed the "plasmosphere." The stainable bodies (NISSL's granules) are present in the plasmosphere, as in the remaining part of the cell-body, but not in the centrosphere. These differences in the structure of the cytoplasm make it possible to distinguish the centrosphere from the remaining structures. The appearance of a radial arrangement of the microsomes originates from the centrosome which lies within the centrosphere (Figs. 3, 7, 8, 9, 10). These radial lines extend from the center into the plasmosphere. The lines are composed of a continuous series of minute protoplasmic corpuscles, smaller than the centrosome, which are known as microsomes (HANSTEIN, 1880). These radial lines formed by the microsomes are covered over very often, in the case of an adult animal, by the great number of the stainable masses which almost entirely obscure the radiations. We distinguish the microsomes from the stainable masses by the fact that the

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<sup>1</sup> Different authors use different terms to designate the structure of the centrosome but the present writer employs the terms which were used by VON LENHOSSÈK—centrosome, centrosphere and plasmosphere. The "centrosome" is a group of minute corpuscles which lie centrally in the centrosphere, or "centralscheibe." The "centrosphere" is the clear transparent area surrounding the centrosome. The "plasmosphere" is the area with coarse protoplasmic granules which surrounds the centrosphere. The plasmosphere grades into the surrounding portion of cell body and is not clearly separated from it. The present writer uses the term "sphere" to designate the entire structure, including centrosphere, radial arrangement of protoplasm and plasmosphere.



microsomes stain intensely with eosin or erythrosin, while the stainable masses do not take a color with those reagents but only with toluidin blue, thionin or methylen blue; that is to say, with the basic stains. The shape of the microsome is nearly circular in its outline, while the stainable masses are generally larger in size than the microsomes and very irregular in outline.

The diameter of the centrosphere is nearly constant measuring  $3.4\ \mu$  to  $4\ \mu$  and being approximately the same in the several groups of the nerve cells. The diameter of the centrosphere is not proportional to the diameter of the cell body in which it lies.

The writer noticed quite often a form of the centrosphere elongated in one axis and measuring  $5\ \mu$  in a long diameter by  $2\ \mu$  in the short diameter. These are probably the regular centrospheres which have become distorted, for if one takes a mean diameter of the two measurements, then the diameter obtained is quite similar to that of the ordinary form, measuring  $3.4\ \mu$  to  $4\ \mu$ .

As has been mentioned already, the general appearance of the centrosphere is quite different from that of the rest of the cell body. This clearness in its appearance is greatly diminished by the growth changes in the cells as the animal matures. This fact will be discussed later on.

The position of the sphere in the cell is variable. Although, it lies, generally, near the nucleus (Figs. 1, 2, 3, 8, 9) in some cases, it may be somewhat removed from it (Figs. 5, 10, 11). The stainable masses are never visible within the centrosphere, and furthermore, the protoplasmic bodies within the centrosphere are more minute than in the remaining part of the cell. These two facts in a large measure account for the clear and transparent appearance to the centrosphere. Besides this, in the protoplasm there are noticeable radial lines that, no doubt, originate from the centrosome which occupies the central position in the centrosphere. The number of the radial lines varies in the different cells.

The minute corpuscles or the centrosome bodies, larger than the rest of the microsomes, are in every case located centrally in the centrosphere. The corpuscle is a somewhat roundish body which stains very deeply with eosin or erythrosin as in the case of the microsomes. The number of the corpuscles which form the centrosome is variable, ranging from one or two (Figs. 1, 2, 3, 5, 7, 8, 9, 10) to a greater number (Fig. 4, 6, 11). Two corpuscles, however, occur in most cases. When the corpuscles occur in great number, they lie close together filling up the central area within a certain limit. It is very doubtful whether we should regard these numerous corpuscles as equivalent to the simpler centrosome composed of one or two corpuscles, because in these cases, the size of the all minute corpuscles is not similar and furthermore, all the corpuscles do not stain with the same intensity, one or two corpuscles which are located most centrally in these groups being distinguishable from the remainder. For this reason, the present writer suggests that some of the corpuscles are nothing more than ordinary microsomes which swell abnormally and are also located accidentally in the neighborhood of the centrosome. This interesting fact will be discussed later. Very often, the writer observed only one corpuscle within the centrosphere (Fig. 7). This appearance has been described by almost all investigators who have studied the centrosome in the nerve cells but this may be due to the fact that the plane of the section passes between the two corpuscles.

Fig. 1 is a section through a spinal ganglion cell of an adult white rat weighing 150 grams. The material was preserved with GILSON's fluid followed by iron hæmatoxylin and bordeaux red. In this case, the sphere lies very close to the nucleus as BÜHLER figured it in a spinal ganglion cell of a frog. The radial arrangements of the protoplasm exist only at the region of the plasmosphere but not within the centrosphere as is the case in the embryonic cell. The centrosphere is somewhat oblong in shape with two conspicuous centrosomes in the central region. This area, "the centrosphere," is clear in its appearance with minute microsomes sometimes densely and

sometimes sparingly arranged but never regularly placed. The above structure of the sphere coincides with that found in other cell groups of the adult rat.

Fig. 2 was drawn from a large pyramidal cell in the cerebral cortex of the adult white rat. Fig. 5 is from a PURKINJE cell of the adult white rat. It is clear from these figures of the two different cells that the structure of the sphere in them is similar to that in the adult spinal ganglion cell.

Fig. 3 represents a large pyramidal cell in a young white rat. This specimen was preserved with the writer's new mixture followed by toluidin blue and eosin. If we compare this figure (3) with the figure 2. which was taken from the same locality of an adult white rat, the structural difference of the centrosphere is plainly seen. In the former case (Fig. 3) the radial arrangement of the microsomes is very conspicuous and unlike the latter case (Fig. 2) in which the internal structure presents a more homogeneous appearance.

Curiously enough, when the centrosome consists of a greater number of corpuscles, then the radial structure of the microsomes within the centrosphere is not clear but rather presents the homogeneous appearance as in the case of the centrosphere of an adult animal. This condition is shown in Figs. 4, 6, 11. The relation existing between the radial structure of the microsomes and the central corpuscles requires further study.

#### IV. HISTORICAL REVIEW OF THE CENTROSOMES IN NERVE CELLS.

The presence of the centrosomes in nerve cells was first announced by VON LENHOSSÈK<sup>1</sup> in the spinal ganglion cells of the frog. It had been previously noticed by several investigators that many spinal ganglion cells, especially the cells in which the nucleus occupied an eccentric position, showed a somewhat concentric arrangement of the protoplasm on the side toward the axone hillock. VON LENHOSSÈK noticed the minute corpuscles which are located in the center of this protoplasmic area

<sup>1</sup> VON LENHOSSÈK.—Centrosome und Sphäre in den Spinal Ganglienzellen des Frosches. *Arch. für Mikr. Anat.*, Band XLVI, pp. 345-368.

and also showed the peculiar characters both of color and of size exhibited by these microsomes. He identified these corpuscles as the centrosome: "Das central Körnchenhauflein, ist ohne Frage identisch mit den Centralkörperchen VAN BENE-  
DEN's." The protoplasmic area which shows a concentric arrangement was called by this same investigator the "plasmosphere." He further distinguished within the plasmosphere, the definite area with a less quantity of the protoplasm and with somewhat transparent appearance, which he termed the "centrosphere." But he does not mention a radial arrangement of the protoplasm.

Soon after VON LENHOSSEK's discovery of the centrosome, many investigators reported their observations on the centrosome in many different classes of animals. The centrosome was found by DEHLER<sup>1</sup> ('95) in the sympathetic ganglion cells of frog; by BÜHLER<sup>2</sup> ('95, '98) in the spinal ganglion cells of the frog ('98) and in the nerve cells in the brain of the lizard ('95); by LEWIS<sup>3</sup> ('96, '98) in the giant nerve cells of an annelid which belongs to the Malduiae; by MCCLURE<sup>4</sup> ('96) in the ganglion cells of *Helix pomatia*; by SCHÄFFER<sup>5</sup> ('96) in the ganglion

<sup>1</sup> DEHLER, A.—Beiträge zur Kenntniss von feineren Bau der sympathischen Ganglienzellen des Frosches. *Arch. für Mikr. Anat.*, Bd. xvi ('95), p. 724-729.

<sup>2</sup> BUEHLER, A.—Protoplasma-structur in Vorderhirn Zellen der Eidechse. *Würzburg*, '95.

BUEHLER, A.—Untersuchungen über den Bau der Nervenzellen. *Königl. Hof.-und Univ. Verlag*, '98.

<sup>3</sup> LEWIS, M.—Centrosome and sphere in certain of the nerve cells of an Invertebrate. *Anat. Anz.*, Bd. xii ('96), S. 291-299.

LEWIS, M.—Studies on the central and peripheral nervous systems of two polychaete annelids. *Proceed. of the American Acad. of Arts and Sciences*. Vol. xxxviii ('98), No. 14.

<sup>4</sup> MCCLURE, C. F. W.—On the presence of centrosome and attraction spheres in the ganglion cells of *Helix pomatia*, with remarks upon the structure of the cell-body. *Princeton College Bulletin*, Vol. viii ('96), No. 2, p. 38-41.

<sup>5</sup> SCHAEFFER, I.—Ueber einen neuen Befund von Centrosomen in Ganglien und Knorpelzellen. *Sitzb. d. Acad. d. wiss. Wien.*, Math.-nat., Cl. '96.

cells of *Petromyzon*; by AYERS<sup>1</sup> ('96) in the motor cells of the electric lobes of *Torpedo*; by VON KÖLLIKER<sup>2</sup> ('97) in adult human giant pyramidal cells; by HAMAKER<sup>3</sup> ('98) in the nervous system *Nereis virens*, SARS; by HOLMGREN<sup>4</sup> ('99) in the spinal ganglion cells of *Lophius piscatorius*; by NELIS<sup>5</sup> ('00) in the spinal ganglion cells of cat, dog, and pig under pathological conditions.

We may add a few words concerning the position of the centrosome. As was mentioned already, VON LENHOSSÈK discovered the centrosome in the concentric protoplasmic area, which is visible in the spinal ganglion in which the nucleus lies eccentrically. These peculiar concentric areas lie on the side of the nucleus toward the axone hillock and at a distance from it. DEHLER has found the centrosome in the same locality as VON LENHOSSÈK, although he has noticed a smaller number of central corpuscles than the former investigator. Recently BÜHLER and HOLMGREN have expressed a view opposed to that of VON LENHOSSÈK, maintaining that the concentric area of the spinal ganglion cells is a locality where the fibrillar structure of the protoplasm which is continuous with the axis cylinder runs from the axone hillock toward the nucleus forming an area in which there appears a somewhat concentric arrangement. They did not find the centrosome in that area but in the immediate neighborhood of the nucleus. According to these investigators, the centrosome as well as sphere of VON LENHOSSÈK are nothing

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<sup>1</sup> AYERS, HOWARD.—The origin and growth of brain cells in the adult body. *Jour. of Comp. Neurology*, Vol. vi ('96), No. 3.

<sup>2</sup> VON KÖLLIKER, A.—Handbuch der Gewebelehre des Menschen. Bd. ii ('97), Leipzig, p. 812.

<sup>3</sup> HAMAKER, J. A.—The nervous system of *Nereis virens*, Sars. A study in comparative neurology. *Bull. of the Mus. of Comp. Zool. at Harvard Coll.*, Vol. xxxii ('98), No. 6, pp. 89-124.

<sup>4</sup> HOLMGREN, E.—Zur Kenntniss der Spinalganglienzellen von *Lophius piscatorius*. *Anatomische Hefte*, Bd. xii, Heft 1, '99.

<sup>5</sup> NELIS, C.—L'apparition des centrosome dans les cellules nerveuses au cours de l'infection rabique. *Le Névaxe*, 1900, Vol. 1, Fasc. 1.

more than the ordinary microsomes which stained accidentally so as to appear similar in color as well as form to the centrosome. The present writer has found the centrosome, in most cases, just near the nucleus as it was described by BÜHLER, HOLMGREN, etc. The eccentric position of the nucleus was noticed very often by the author. The centrosome, however, occurs not only in such a cell but also the cells with centrally located nuclei. From this observation, we can say that the position of the nucleus is not of primary importance for the occurrence of the centrosome.

The number of the central corpuscles or centrosomes in the strict sense of the word has been given differently by different investigators. VON LENHOSSÈK has counted numerous corpuscles within the centrosphere to which collectively he gave the name of centrosome. DEHLER and MISS LEWIS have also noticed several corpuscles, although they counted only one or two in some cases. BÜHLER is the first investigator to give the number of the corpuscles forming the true centrosome as two. NELIS<sup>1</sup> observed that the centrosome is composed of only one corpuscle in a resting state. When the cells are preparing to divide, however, under certain conditions, the centrosome may also divide into two. Very often he has found the two centrosomes in the cells one on each side of the nucleus. The present writer noticed that the centrosome consists of two minute corpuscles in most cases, but many corpuscles occur occasionally, and in one instance there was only one. In the preceding chapter it was stated that when the centrosome is formed of many corpuscles the structure of the centrosphere is modified in such a manner that the protoplasmic relations in the centrosphere become invisible and it presents a homogeneous appearance as shown in the adult nerve cells, the centrosphere being filled with microsomes. In this case, the radiation in the plasmosphere is either destroyed or it still retains its characteristic arrangement as far as these preparations are concerned.

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<sup>1</sup> NELIS stated that the centrosome is wholly invisible in the resting state of nerve cells, but under certain stimulation it may appear, in which event it is composed of one corpuscle.

VON KÖLLIKER is the first to report the centrosome in the mammalian central nervous system. He found the centrosome in a giant pyramidal cell of the posterior central gyrus of a man thirty years old. Later, NELIS demonstrated the presence of the centrosome in the nerve cells of some adult higher mammalia, but only under pathological conditions. He summarizes his observations as follows: "A l'état normal, un centrosome n'est pas visible dans les cellules nerveuses des mammifères. Le processus pathologique rabique détermine l'apparition du centrosome dans les cellules nerveuses des ganglions spinaux chez le chien et chez le lapin. Au cours de cette infection, le centrosome ne reste pas inerte; il semble se diviser; en deux; les deux centrosomes tendent à se séparer et à émigrer dans deux directions opposées.

"Les modifications nucléaires des cellules nerveuses au cours de l'infection rabique représentent pour nous des phénomènes de régression, d'atrophie, précédés d'une tendance à la proliférations qui avertit prématurément, tendance se traduisant uniquement par l'apparition du centrosome au sein du protoplasme, sa division probable et le commencement de migration des deux centrosomes nouvellement formés."

He absolutely denied the presence of the centrosome in mammalian nerve cells in a normal condition as far as his observations went. He further mentioned a possibility of the division of nerve cells in the mature animals, although he has not actually observed it. On the other hand, MISS LEWIS' observations led her to doubt the dividing process in the adult nerve cells. But she does not base her statement upon the structure of the centrosome but on the fact that she has not noticed such cases of division although she has examined the preparations made from more than a dozen worms. The present writer also doubts the occurrence of division (mitotic) of matured normal cells in the normal condition for the following reasons: The sphere in an adult nerve cell is slightly different from that of young nerve cells. The centrosome in young cells shows a clear outline with a radial arrangement of the protoplasm, the radii originating from the central corpuscles or centrosome. The

clear space, or centrosphere, which surrounds the centrosome shows a definite figure in young cells. The structures above mentioned, however, are not to be seen when the cell attains a mature stage, and the radial arrangement of the protoplasm within the centrosphere not only becomes invisible, but the clear area, or centrosphere itself, also is diminished more or less in its diameter. In some cases, the radial arrangement of the protoplasm in the region of the plasmosphere is entirely absent (Fig. 11). These structural differences between an adult and young stage signify, no doubt, the slow atrophy of the sphere. If my statement is true, we can hardly imagine that the centrosome which is in process of degeneration may undergo division in a normal condition. The writer has examined a large number of the nerve cells of the white rat in which the centrosome is nicely demonstrable but has not noticed even a slight trace of the process of division.

These observations raise the whole question of the division of mature nerve cells.

The current theory claims that after a nerve cell once sends out its axis cylinder it is incapable of division or further reproduction. It is known, however, in the case of another kind of tissues, that under a certain pathological condition the matured cells produce daughter cells by the dividing process, either mitotic or amitotic. This phenomenon has been reported in the nerve cells also, but in our opinion the results are not fully established. TEDESCHI<sup>1</sup> who studied the results of intoxication on the mammalian body has observed the presence of karyokinetic division in the adult nerve cells. According to him this phenomenon occurs three days after the poisonous substance has been introduced into the body. Later NELIS<sup>1</sup> suggested the possibility of the division of an adult nerve cells under the

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<sup>1</sup> TEDESCHI, A.—Anatomische-pathologische und experimentelle Untersuchungen über die Regeneration des Nerven Gewebes. *Vergl. Mith. Centralbl. f. allg. path. u. path. Anat.*, Jena, Bd. viii ('96), p. 449-451. Also Anatomische experimentellen Beiträge zum Studien der Regeneration des Gewebe des Centralnervensystem. *Beitr. z. path. anat. u. z. all. path.*, Jena, '97, Vol. xxi, p. 43-72.

<sup>1</sup> NELIS, C.—Loc. cit.



pathological condition. He said "Au cours cette infection, le centrosome ne reste pas inerte, il semble se diviser en deux, les deux centrosomes tendent à se séparer et à émigrer dans deux directions opposées."

Recently some very interesting papers have appeared concerning the reproduction of the nerve cells. AYERS,<sup>1</sup> who is one of the authors, has summarized the observation made on the electric lobes of Torpedo, in his preliminary report, as follows:

"(1). Large motor cells (electric lobes), not to be distinguished from the ordinary functional cells except by the size of the nucleus and cell-body.

"(2). Cells of the same size as (1) but with two nuclear bodies. Both may be close together in the center of the cell or widely separated and lying near the periphery of the cell.

"(3). Cells showing an evident constriction of the protoplasmic body between the nuclei as though about to divide.

"(4). Double cells with short connecting bar which are usually large and band-shaped.

"(5). Double cells in which the connecting bar is drawn out into a thin filament, tapering conically from either cell-body towards the other.

"(6). Since each nerve cell of the brain and ganglia has a perilymphatic capsule surrounding it, when the cell-body is cut into two the perilymphatic space is not at once doubled but the two cells still lie in a common cavity. Because of this it is possible to trace the genetic relation of these electromotor cells even after they have completely separated by the breaking of the connecting bands, as in those cases where the nerve cells become completely separated. Ultimately, of course, the lymphatic spaces divide also by completing the capsular wall close about each cell."

The writer has noticed the same appearance as those described by DR. AYERS. Here, however, arises the very difficult question of interpretation, whether these cells which are

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<sup>1</sup> AYERS, H.—Loc. cit.

apparently dividing are remnants of imperfect division of embryonal germ cells which have become functional in such a condition without any further morphological changes, or whether, on the contrary, they are formed by the division, either mitotic or amitotic, of functional adult cells under special conditions. If the foregoing supposition is true, then the phenomenon of the continuity of the nerve cell bodies does not prove the division of the nerve cells in a matured condition. Since at the present moment there is not the slightest direct evidence for the amitotic division of nerve cells, we are justified in demanding that good evidence of mitosis as shown by the condition of the nuclear substance, be brought forward—if these cells are to be considered as actually dividing. This has not been done.

In order to give a positive answer to the questions above mentioned, it seems to me that the only safe and reliable method consists in counting the nerve cells in the spinal ganglia of a given species of animal at different ages and thus determining whether there is any increase in their number. The present writer is trying this method under the direction of PROF. DONALDSON, and hopes to report in the near future. We can only say, at present, concerning the division-problem that the nerve cells in vertebrates as well as invertebrates have the centrosome and the sphere, which are regarded as the dynamic centers of the mitotic division and further that this centrosome is able to take the first steps of division under a certain forms of stimulation, as has been observed by some investigators; but in the normal state the centrosome in an adult nerve cell presents slight morphological differences from that of the embryonic cell, which we interpret as the beginning of degeneration.

#### V. SUMMARY.

(1). Several classes of nerve cells in the young rat, as well as adult rat, have a centrosome and attraction sphere.

(2). The centrosome in the young rat is more easily distinguished from the rest of the structures than that in the adult.

(3). The sphere is nearly the same in size throughout the different classes of the nerve cells in the same animal and the size does not alter with the age of the cell.

(4). In most cases the centrosome is composed of two corpuscles, but more than two rarely, and sometimes of only one.

(5). The centrosome in an adult rat shows a slight tendency to degenerate when compared with that of the rat at birth.

#### VI. ILLUSTRATIONS OF THE CENTROSOME IN THE NERVE CELLS OF THE WHITE RAT.

The following pictures are free-hand drawings, the enlargements of the drawings being dissimilar. The actual size of the cells is however, given in the case of each figure, and by the aid of these measurements the cells can be compared.

#### PLATE II.

*Fig. 1.* Spinal ganglion cell of an adult white rat. Cell-body,  $55 \times 39 \mu$ ; nucleus,  $17 \times 14 \mu$ . GILSON's fluid.

*Fig. 2.* Large pyramidal cell of an adult white rat. Cell-body,  $23 \times 19 \mu$ ; nucleus,  $13 \times 12 \mu$ .

*Fig. 3.* Giant pyramidal cell of a young white rat. Cell-body,  $17 \times 10 \mu$ ; nucleus,  $11 \times 8 \mu$ .

*Fig. 4.* Corpus dentatum of a young white rat. Cell-body,  $19 \times 13 \mu$ ; nucleus,  $11 \times 8 \mu$ .

*Fig. 5.* Purkinje cell of an adult white rat. Cell-body,  $21 \times 17 \mu$ ; nucleus,  $12.5 \times 9 \mu$ .

*Figs. 6-10.* Purkinje cells of a young white rat. Cell-bodies,  $15 \times 11 \mu$ ; nuclei,  $9 \times 8 \mu$ —mean diameters.

*Fig. 11.* Spinal ganglion cells of an adult white rat. Cell-body,  $40 \times 44 \mu$ ; nucleus,  $15 \times 15 \mu$ .

From *Figs. 2-11.* The materials were preserved with the author's new mixture.

## THE OPTIC LOBES AND OPTIC TRACTS OF AMBLY- OPSIS SPELÆUS DEKAY.<sup>1</sup>

By EARL E. RAMSEY.

With Plates III and IV.

*Amblyopsis spelæus* is one of the blind fishes inhabiting the caves of the Ohio Valley. It is occasionally found in Mammoth Cave and in the surrounding caves. It is locally abundant in the caves north of the Ohio River. The specimens examined were taken near Mitchell, Indiana.

The eye of *Amblyopsis*, according to Eigenmann (Roux-Archiv, VIII) is a mere vestige. It is a solid ball of cells with no vitreous body and probably no lens, with the ganglionic layer forming a solid funnel-shaped mass of cells passing through the center. In the adult, the optic nerve has not been successfully traced to the brain either by dissections or by means of sections. What is left of the optic nerve in the adult forms a flocculent strand of tissue that can be followed but a short distance beyond the eye. *Amblyopsis* passes its entire life in total darkness. It is extremely doubtful whether light impressions could be received by the eye and transmitted to the brain, even if adult *Amblyopsis* should be brought to the light. However that may be, it seems quite certain that the specimens, whose optic lobes served as the basis of this paper, had spent their lives in the caves and their optic lobes had no opportunity of functioning as the central organ of sight, even if there is a nervous connection with the eye.

A comparison of the macroscopic appearances of the brain of a normal fish and that of the blind fish, *Amblyopsis spelæus* Dekay, discloses a number of interesting conditions. The optic lobes and the optic tracts are measurably degenerate. The

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<sup>1</sup> Contributions from the Zoological Laboratory of the Indiana University, No. 44. C. H. Eigenmann, director.

hemispheres are larger in *Amblyopsis* than in the average of normal brains. The brains of *Campostoma anomalum*, *Percina caprodes*, *Eupomotis gibbosus* and *Amblyopsis* were measured with regard to the comparative widths of the optic lobes and the hemispheres. Five fishes of the same length were taken of each species. The averages obtained are as follows :

	<i>C. anomalum</i>	<i>E. gibbosus</i>	<i>P. caprodes</i>	<i>A. spelæus</i>
Opt. lobes	5. mm	5. mm	6.4 mm	3.2 mm
Hemisph.	2.8 mm	3.7 mm	3.5 mm	4. mm
Comp. widths	56%	74%	54%	125%

It is thus seen that the hemispheres are relatively larger in the blind fish than in the more normal forms, and that the optic lobes are relatively much smaller in the former.

There is no noticeable variation in the cerebellum. In length there is a marked shrinkage, chiefly in the optic lobes as shown by the position of the cerebellum, which lies directly on the lobes (Fig. 3, V). In the normal brain, the cerebellum is situated well back, hardly reaching the lobes (Fig. 5, V). The following table gives an idea of the length of the brain as compared with the length of the fish. The brain length is measured from the tip of the olfactory lobes to the posterior part of the cerebellum :

Species	Length body	Length brain	%	Average %
<i>Amblyopsis</i> 1	92 mm	5.5 mm	6. %	6.3%
" 2	80 mm	5.3 mm	6.6%	
" 3	90 mm	5.5 mm	6. %	
" 4	88 mm	5.8 mm	6.6%	
" 5	80 mm	5.2 mm	6.5%	
" 6	100 mm	6. mm	6. %	
<i>Campostoma</i> 1	88 mm	8.5 mm	9.6%	9.8%
" 2	103 mm	9. mm	8.7%	
" 3	72 mm	7.5 mm	10. %	
" 4	68 mm	7. mm	10. %	
" 5	58 mm	6.3 mm	10. %	

The result shows the brain of *Amblyopsis* to be only two thirds as long as that of *Campostoma*. This shrinkage in width and length is great enough to show itself in the extent to which the cranial cavity is filled. A great depth of fatty tissue covers

the dorsal surface of the brain. The only other external modification of any note is the absence of either optic nerves or optic chiasma.

*Internal Structure of Optic Lobes.*

The optic lobes are normally composed of seven layers which are, from outside to inside, as follows :

- (1). A peripheral zone.
- (2). An optic fiber layer from the optic nerve.
- (3). An optic cell layer.
- (4). A deep cell layer. According to KRAUSE this layer contains in its outer part the cells which serve as terminal stations for the optic nerve, and in its inner sub-layer the end stations for the fifth layer (Marklager).
- (5). A deep fiber layer.
- (6). A granular layer.
- (7). The ependyma and its epithelium, which lies next to the ventricle of the lobes.

The optic lobes of Amblyopsis show a marked degeneration. The dorsal walls are not more than one-half or two-thirds as thick as in the normal brain. Its contour is so flattened that the ventricle is almost obliterated (Fig. 8, 16). The torus longitudinalis, which in the normal brain is suspended in the ventricle in the median line entirely below the layers of the lobes is *between* the lobes and on nearly the same level with them. The torus thus forms a commissure connecting the lobes. The band of fibers connecting them dips downward in the normal brain and crosses to the opposite side through the torus; in the degenerate lobe, they cross from one side to the other in almost a straight line (Fig. 8, 15). The shrinkage in length is shown in the fact that the hypophysis is crowded forward to the anterior level of the lobes (Fig. 7, 12).

The optic nerve of the normal brain is derived from the second and fourth layers of the lobes. The fibers of the second layer pass downward on both sides of the lobes and the inner ones cross over at the ventral surface where they join the fibers of the same layer from the outer side. They then con-

tinue forward and downward to the optic chiasma as the optic tracts. The fifth layer is composed of diagonal fibers and descending fibers. These latter nerves pass downward and become a part of the optic tract (Fig. 6, 5).

As has been said, the wall of the optic lobes of *Amblyopsis* has undergone considerable shrinkage in thickness. The outer layer is not changed. The second layer, which is derived from the optic nerve, is entirely wanting. The optic nerve is represented by a small bundle of tissue, which is probably the remnant of the neurilemma. In the brain where the second layer should be, there is a narrow space containing practically no tissue. The third layer is unchanged. The fourth layer consists normally of two sub-layers; the outer one has both nerve fibers and nerve cells,—the latter according to KRAUSE being the terminal stations of the optic nerve—and the inner sub-layer has the terminal stations of the fifth layer in it. The outer sub-layer is entirely atrophied in the lobes of the blind fish, and the inner one, if at all present, is indistinguishable from the third layer (Fig. 8, 3 and 4).

The fifth layer is reduced to diagonal fibers. The descending fibers which join the optic tracts are atrophied. The diagonal fibers are more apparent than in the normal brain. These fibers form a broad commissure in the torus longitudinalis which runs laterally to the outer edge of the lobes where it turns back into the substance of the brain just beneath the ventricle and becomes diagonal. Cross sections of its fibers arising from various levels of the lobes are shown in (Fig. 8, 5).

The sixth layer is a granular layer. Its thickness is less than in the normal brain. No other change is noticeable. The thickness of the seventh layer, ependyma, is not more than half that of a normal brain. The cells show some shrinkage.

The differences in the lobes thus appear to be: first, in the atrophy of the second layer; second, the outer sub-layer of the fourth layer is entirely gone; third, the descending fibers of the fifth layer are wholly wanting; fourth, the granular layer is not so thick and the ependyma is not only thinner but reduced in the number of its cells.

The optic tracts, that portion of the nervous tissue which lies between the optic lobes and the optic chiasma, are entirely wanting. The space occupied by these tracts in the normal brain (Fig. 8, 7) is, in this brain, partially occupied by tissue in which I have not been able to make out any structure. All the stains that have been tried have failed to reveal any cells. These tracts do not take the stains with the same readiness and in the same degree that normal brains do when subjected to exactly the same treatment. Three fish, the *Amblyopsis*, *Campostoma* and *Eupomotis*, were killed and the heads placed in FOHL's mixture for the same time. The brains were then removed from the skull as soon as they were sufficiently hardened. They were then placed in the same bottle in order that the conditions might be the same. The three were imbedded in the same block, and sectioned side by side. The tissue of the tracts of the brains of *Campostoma* and *Eupomotis* differentiated very well—but the degenerate brain showed no structure.

In the dissections of the head of the blind fish, I have been unable to find any indications of optic nerves leaving the lobes. In both the dissections and the sections which have been made of the entire head and brain, there seems to be no break in the enveloping membranes on the anterior ventral surface of the lobes where the optic nerves originate. The vestiges of the optic nerve can be followed backward from the eye for a short distance. The only tracts leading away from the lobes are those which connect them with cerebral hemispheres and cerebellum. Those which pass forward to the hemispheres are from the diagonal fibers of the fifth layer. These pass laterally, but before reaching the lateral aspect of the lobes turn downward through the granular layer and epithelial layer, and then course forward toward the ventral surface of the hemispheres.



*Methods.*

1. The most successful method used is as follows. The brain is fixed in FOHL's mixture of picric, osmic, platinic and acetic acids for from three to four days. It is then put into pyroligneous acid for two days. It is next washed in wood alcohol until the alcohol is no longer tinged yellow. After being dehydrated in the usual way, it is saturated in chloroform and imbedded in paraffin, after which it is sectioned and mounted in balsam. The acids serve as stains as well as fixing agents, and differentiate the various structures excellently.

2. For other phases of the work, the following was found good:

Fish were killed by cutting the spinal cord just back of the medulla. The large blood vessels are cut while the heart still beats, that as much blood as possible may be drained away from the brain. The blood corpuscles give a very deceptive appearance when stained in the vessels penetrating the brain. Before placing the brain in alcohol, cut away as much of the head as possible without injuring the brain. This allows the alcohol to penetrate uniformly and prevents the brain from becoming colored, as it does when the surrounding tissue is not removed. The head then is placed in 35, 50, 70, 85, and 95 per cent. alcohols for twelve to sixteen hours in each grade. The brain is easily removed from the head and placed in absolute alcohol for four or five hours. It should *not* show any shriveled appearance, as it will if fixed in a high grade of alcohol at once. It is now put in choloform until it sinks, when it is put in the paraffin bath, and imbedded. Sections are cut with a sliding microtome, the sections alternating 15 and 20  $\mu$ , since some points are more easily made out in the 15  $\mu$  sections, while others are best found in those 20  $\mu$  thick. They are fixed by the distilled water method. The paraffin is removed with xylol and the slide washed with 95 per cent. alcohol for a minute or two to remove the xylol. The slide is placed in the stain, which is prepared as follows: Dissolve 0.3 g. dry methelyn-blue in 250 cc. distilled water. Add to this 0.1 g. or 0.2 g. of any good un-

colored castile soap. Allow this to dissolve and filter the mixture. Place the slide in a crystallizing dish which contains the stain. Set the dish on a bath or stove where its temperature can be kept at from 55 to 60 degrees C. Four or five hours is sufficient to stain the sections, although they do not overstain easily. A differentiating fluid is made from 90 parts absolute alcohol and 10 parts aniline oil. When no more blue color is given off, the sections may be cleared in oil of cajeput, and mounted in xylol balsam. So far, I do not find that this mounting medium affects the stain.

Nerve cells and their processes should show a rich blue stain, and their nuclei a yet darker stain. Fibrous tissue should remain unstained, but can be followed with ease, as the tissues are well preserved. Fresh tissue is required to begin with, as old tissue *fails* of differentiation. Good, clear outlines of ganglionic cells can be obtained, even with an oil immersion lens, in the 20  $\mu$  sections.

#### EXPLANATION OF FIGURES.

##### REFERENCE LETTERS.

- I. Olfactory nerve.
- II. Olfactory lobes.
- III. Cerebral hemispheres.
- IV. Optic lobes.
- V. Cerebellum.
- VI. Fourth ventricle.
- VII. Medulla oblongata.
- VIII. Spinal cord.
- IX. Otolith.
- X. Various cranial nerves.
- XI. Pituitary body.
- XII. Lobi inferiores.
- XIII. Saccus vasculosus.
  - 1. First layer of optic lobe.
  - 2. Degenerate optic fiber layer.
  - 3. Optic cell layer.
  - 4. Deep cell layer.
  - 5. Deep fiber layer.
  - 5a. Diagonal fibers of deep fiber layer.
  - 6. Granular layer.

7. Optic tracts.
- 7a. Optic tract region.
8. Optic lobe cut so that it shows but layers 1 and 2.
9. Nucleus opticus lateralis.
10. Epithalamus.
11. Posterior commissure.
12. Hypophysis.
13. Ependyma.
14. Inferior lobe.
15. Torus longitudinalis.
16. Ventricle.

PLATE III.

*Fig. 1.* Dorsal view of the brain of *Amblyopsis spelæus* Dekay. Photograph of a dissection of head of a specimen 100 mm. long ( $\times 2.8$ ).

*Fig. 2.* Photograph of the head of *Amblyopsis* 35 mm. long ( $\times$  about 16.3) cleared in xylol. To show the degree of degeneration of the eyes.

PLATE IV.

*Fig. 3.* Dorsal view of the brain of a specimen of *A. spelæus* 100 mm. long ( $\times 7.7$ ).

*Fig. 4.* Ventral view of the brain of a specimen of *A. spelæus* 85 mm. long ( $\times 11.2$ ).

*Fig. 5.* Dorsal view of the brain of a specimen of *Campostoma anomalum*, 85 mm. long ( $\times 7.7$ ).

*Fig. 6.* Cross section of brain of *C. anomalum* near the anterior portion of the optic lobes ( $\times 24.5$ ). Specimen 75 mm. long.

*Fig. 7.* Cross section of the brain of *A. spelæus* in the same relative position as the section in Fig. 6 ( $\times 37$ ). Specimen 77 mm. long.

*Fig. 8.* Cross section of the brain of *A. spelæus* through the middle of the optic lobes ( $\times 52.5$ ). Specimen 77 mm. long.

## THE RAMI OF THE FIFTH NERVE IN AMPHIBIA.

By G. E. COGHILL.

With Plate V.

In a study of the components of the cranial nerves of *Amblystoma* I have found very suggestive relations existing between the ramus ophthalmicus profundus V and the ramus palatinus VII. This observation has led me to review the conditions generally described in Amphibia, and to my own mind the *Amblystoma* is extremely helpful in interpreting the relations between certain rami of the fifth nerve in Urodela on the one hand and the Anura on the other.

My observations upon *Amblystoma tigrinum* have been made from serial sections of the heads of larvae of different ages and of the adult head also. The series were cut transversely ten micra thick, and in both planes longitudinally. Those of the larva were hardened in FLEMMING'S stronger solution, diluted in some cases, and stained on the slide after WEIGERT. The adult head was stained *in toto* according to vom RATH. For comparison I have made also a series, cut transversely, of the head of a larva of *Rana* at a stage some time previous to the appearance of the hind limbs. This series is absolutely continuous through the region in question and is satisfactorily stained with the WEIGERT method after fixation of FLEMMING'S stronger solution. It has enabled me to supplement STRONG'S description of the "accessory rami" of the trigeminus and to show their relation to certain nerves in *Amblystoma*.

In *Amblystoma* the lateral line ganglion of the seventh nerve, associated with the Gasserian ganglion, is microscopically distinguishable from the latter. It gives off two rami which arise in close contact with one another from the most dorsal portion of the common ganglionic mass. In the adult these

nerves arise wholly separate from any branch of the Gasserian ganglion, and are, therefore, in their proximal portions purely lateral line nerves. In some larval heads I have examined, these nerves are more obscure in their relations than I find them in the adult.

One of these lateral line nerves is the superficial ophthalmic VII (Fig. 4, *os*). It passes laterad out of the cranium in company with other branches from the Gasserian and lateral line ganglion, between the muscles masseter and temporalis, then meso-cephalad subcutaneously mesal of the eye. It innervates the supra-orbital lateral line organs. It is intimately associated with a twig from the ophthalmicus profundus V over the nasal septum, but in no case have I found a true anastomosis between these nerves. The ophthalmicus superficialis VII is, therefore, a purely lateral line nerve throughout.

The other nerve issuing from the lateral line ganglion in close relation with the superficial ophthalmic is the ramus buccalis VII. It at first follows a course ventral of the superficial ophthalmic VII, and as it passes out of the cranium fuses with a general cutaneous nerve from the Gasserian ganglion (Fig. 4, *b*). The resulting nerve will be discussed below.

The dorso-lateral portion of the Gasserian ganglion gives rise to the ramus mandibularis V, which, farther than its origin from the ganglion and its relation to the nerve which joins the buccal VII, has no bearing on the present discussion.

From the ventral portion of the Gasserian ganglion the ophthalmicus profundus V passes directly cephalad, and, after giving off numerous branches of no special significance here, divides in the region of the optic nerve into three terminal branches. These nerves I designate, for purposes of this discussion, as the lateral, mesal and ventral terminal branches of the ophthalmicus profundus V (Fig. 1, *ol*, *om*, *ov*).

The mesal terminal branch of the ophthalmicus profundus (Fig. 1, *om*) inclines mesad to a position dorsal of the muscle obliquus superior and mesal of the olfactory epithelium, near the dorsal wall of the olfactory capsule. Within the capsule it gives off several twigs which penetrate the roof of the cap-

sule and are distributed to the skin dorsal of the latter and near the tip of the snout. The terminal twigs of the mesal nerve ultimately reach the skin mesal of the external nares.

The lateral terminal branch (Fig. 1, *ol*) sends a twig to the anterior canthus of the eye, and innervates the skin anterior, not ventral, of this point. In one case I have observed a twig from this nerve anastomosing with a twig from the mesal terminal branch of the ophthalmic, and the resulting nerve going to the skin lateral of the external nares. Terminal twigs of the ophthalmic always innervate the region traversed by the buccalis VII, but they never enter the area innervated by the general cutaneous nerve which accompanies the buccal proximally.

The ventral terminal branch of the ophthalmic (Fig. 1, *ov*) passes ventral of the olfactory epithelium into the region of the palatinus VII which approaches it near the caudal aspect of the internal nares. As the two nerves approach each other both divide (Fig. 1, *p, o*). One division of the ventral ophthalmic branch fuses with the lateral division of the palatine (*lp*) and passes laterad immediately caudal of the internal nares (*u*). A part of the resulting nerve inclines caudad, and the remainder turns cephalad along the lateral aspect of the internal nares and innervates the region lateral and anterior of this point. The other division of the ventral ophthalmic branch, in close relation with the mesal division of the palatine, passes cephalad along the mesal aspect of the internal nares (Figs. 1, 4D, *mp*). The two nerves soon fuse and the resulting nerve innervates the region anterior of the vomers.

The remaining nerve (Fig. 4A, *ac*) which concerns this discussion is that branch of the fifth nerve which arises from the dorso-mesal portion of the Gasserian ganglion and mesal of the origin of the mandibularis (*m*). It is a nerve of about the same magnitude as the buccalis VII with which it fuses as it emerges from the cranium. The resulting nerve passes laterad ventral of the ophthalmicus superficialis VII, and turns cephalad around the border of the temporalis muscle to a position ventral of the eye. Near its flexure about the muscle it sends

off to the skin of the vicinity a large twig composed of lateral line and general cutaneous fibers. Near this point also the nerve frequently separates into several bundles of fibers which unite again into a common trunk. Other twigs of varied composition are given off in this vicinity, but a general cutaneous twig to the region immediately posterior of the eye and another of the same composition to the under eyelid seem to be constant.

Near the caudal region of the eye this nerve divides into a general cutaneous nerve (Fig. 4C, *ac*) which innervates the lip anterior and ventral of the eye, and a lateral line nerve (*b*) which innervates the line of organs passing ventral of the eye and around the border of the snout. This nerve is the buccalis VII. It seems to me certain that there is at this point of division a complete separation of the general cutaneous from the acustico-lateral component.

In the larva of *Rana* we find the ophthalmicus superficialis VII holding practically the same relation to the ganglion and to the other nerves proximally as described for *Amblystoma*, but it passes more directly cephalad in *Rana* and becomes separated from the other rami much sooner than in *Amblystoma* (Fig. 3, *os*). The ramus buccalis VII, however, passes around the anterior border of the ear capsule in company with the rami from the Gasserian ganglion in essentially the same relation to them as the buccalis holds to the corresponding nerves in *Amblystoma*. And, like the buccalis of *Amblystoma*, the buccalis of *Rana* soon fuses with a general cutaneous nerve from the Gasserian ganglion (Fig. 3, *b, ac*). The further course of the nerve will be considered below.

Arising from the latero-dorsal region of the Gasserian ganglion in *Rana* we find the maxillo-mandibularis instead of the mandibularis as in *Amblystoma*, and from this the maxillaris nerve arises at the transverse level of the eye (Figs. 2, 3, *m, mx*). The maxillaris gives off a branch ventrally (Fig. 2, *mxv*) which anastomoses with the lateral division of the palatinus VII (Fig. 2, *lp*) in the roof of the mouth near the postero-lateral aspect of the internal nares (*n*). The resulting nerve continues

cephalad along the lateral aspect of the internal nares (Fig. 3D, *x*) and is distributed to the antero-lateral areas of the roof of the mouth. The remainder of the maxillaris trunk continues its course cephalad wholly lateral of the olfactory epithelium and is distributed to the skin between the eye and the external nares (Fig. 3D, *mx*). I can find no fibers of the maxillaris going to the eyelids. The region innervated by the nerve corresponds with a part of the region innervated in *Amblystoma* by the lateral terminal branch of the ophthalmicus profundus (Fig. 4D, *ol*). Moreover, the oral region innervated by the maxillaris through anastomosis with the lateral division of the palatinus VII corresponds with the oral region innervated in *Amblystoma* by a part of the ventral terminal branch of the ophthalmicus through anastomosis with the lateral division of the palatine.

In perfect accord with the facts just cited we find that in the larva of *Rana* the ophthalmicus profundus V, in its origin like that of *Amblystoma*, after giving off several sensory and motor twigs, breaks up into two terminal branches, the lateralis narium to the skin immediately caudal of the external nares, and the medialis narium which passes dorsal of the olfactory epithelium and sends a branch, the ramus communicans cum N. palatino, ventrad to anastomose with the mesal division of the palatinus VII which approaches it from along the mesal aspect of the internal nares (Figs. 2, 3, *mp*). By this anastomosis the oral region is innervated which corresponds to the region innervated in *Amblystoma* by a part of the ventral terminal branch of the ophthalmicus profundus through anastomosis with the mesal division of the palatinus VII.

Reviewing from another standpoint the conditions just described, we see that the ramus palatinus VII in both *Rana* and *Amblystoma* forms into two terminal branches, one of which passes on either side of the internal nares (*mp*, *lp*). In *Amblystoma* both of these branches anastomose with the ophthalmicus profundus while in *Rana* the mesal division anastomoses with the ophthalmic and the lateral division with the maxillaris V. Within the oral cavity, therefore, the function of the maxillaris



V of *Rana* is performed in *Amblystoma* by the ophthalmicus profundus.

In the light of these facts it becomes impossible to homologize the ventral terminal branch of the ophthalmicus profundus in *Amblystoma* with the ramus communicans cum N. palatino in *Rana*. The former nerve is the equivalent of two nerves in *Rana*, the ramus communicans cum N. palatino of the ophthalmicus and that of the maxillaris.

It is a noteworthy fact, also, that in *Rana*, according to GAUPP, the maxillaris nerve, in union with fibers from the ophthalmic, innervates the muscle levator bulbi. In *Amblystoma* this muscle is innervated wholly by the ophthalmic. This is not only another case where the functions of the ophthalmicus profundus in *Amblystoma* are carried over to the maxillaris in *Rana*, but it shows that in *Rana* there is an intimate relation between the maxillaris and ophthalmic nerves, a relation which exists between the general cutaneous as well as between the motor components of the nerves as shown by the anastomoses between the terminal sensory twigs of the two nerves described by GAUPP.

An unqualified homology can not be established between the two species with reference to the other terminal branches of the ophthalmicus profundus. The lateralis narium of *Rana* is certainly not homologous with the lateral terminal branch of the nerve in *Amblystoma*, for the latter nerve innervates a region belonging, at least in the greater part, to the maxillaris in *Rana*. Exact homologies in this region can be established only by far more extensive comparative and perhaps embryological data than have yet been compiled.

The nerve which has usually been called the maxillaris in Urodela is of special interest in this connection. The discovery of a lateral line component in this nerve forced it out of complete homology with the maxillaris of *Anura*, but some anatomists have called its general cutaneous component the maxillaris. A comparison of this nerve with Strong's lateral "accessory ramus" of the trigeminus as to origin and distribution is quite conclusive.

According to my preparation the lateral and larger "accessory ramus" arises, as Strong describes it, from the dorso-mesal portion of the Gasserian ganglion. It passes across the dorsal surface of the maxillo-mandibularis and passes around the anterior border of the ear capsule ventral of the buccalis VII (Fig. 3, *ac, b, m*). The buccalis VII and "accessory ramus" pass laterad close together to near the lateral border of the suspensorium. In this position the two nerves are fused for a short distance. Farther cephalad the buccalis holds its usual infra-orbital position. The "accessory ramus" follows close along its lateral aspect to a position ventral of the eye (Fig. 3C, *b, ac*).

Soon after separating from the buccalis VII the "accessory ramus" sends off a large branch which passes laterad and cephalad to the skin of the cheek caudal of the eye. Ventral of the eye it sends another branch to the skin of the cheek, and a small twig to the lower eyelid. Ventral of the anterior part of the eye there appears, in close relation with the buccalis VII, a small nerve which arose from the "accessory ramus" a short distance ectal of the Gasserian ganglion and, traversing the surface of the facial muscles, distributes itself to the skin antero-ventral of the eye.

This general cutaneous branch of the trigeminus, therefore, innervates in the larva of *Rana* the region corresponding to that in *Amblystoma* innervated by that nerve from the Gasserian ganglion which is fused with the buccal VII. These nerves correspond also in their origin, arising in both cases from the dorso-mesal portion of the Gasserian ganglion and passing across the dorsal surface of the mandibularis in the one case and the maxillo-mandibularis in the other. They correspond also in the relation to the buccal VII, the extent of the fusion being exceedingly reduced in *Rana*. They correspond also in other details which need not be discussed here. We must conclude, therefore, that the "accessory ramus" of the trigeminus in the tadpole is homologous with the general cutaneous portion of the so-called maxillaris in *Amblystoma*. This

being the case, we have in Amphibia an infra-orbital nerve of acustico-lateral and general cutaneous composition.

The relations of this infra-orbital nerve in the adult *Rana* seem to be but partially known. The acustico-lateral component degenerates with the disappearance of the lateral line organs. The general cutaneous component probably persists as the rami zygomatico-temporales and palpebrales inferioris as described by GAUPP. The relation which the nerve holds to the maxillo-mandibularis in older tadpoles suggests the possibility of a more extensive fusion of the nerve with that trunk so that the at one time independent twig might later become a ramus of the maxillaris. It is quite certain, at any rate, that the region innervated in the adult by the rami mentioned is not touched by the maxillaris of the larva but is innervated by the "accessory ramus."

Although the relations existing in other Amphibia between the ophthalmicus profundus, the maxillaris, and the palatinus VII have received but incidental notice by anatomists generally, a brief review of the subject may be helpful.

In *Siredon pisciformis* (larva of *Amblystoma*) FISCHER describes the ventral terminal branch of the ophthalmicus profundus (his nasalis) as issuing from the lateral terminal branch of that nerve. He finds the anastomosis of the ventral branch with the palatinus VII, and describes the nerve resulting from that anastomosis as passing cephalad over the vomer essentially as I find the mesal nerve derived from the double anastomosis. The anastomosing nerves which pass laterad immediately caudad of the internal nares escaped his notice. The infra-orbital nerve, which I have described as composed of acustico-lateral and general cutaneous components, Fischer calls the maxillaris superior of the trigeminus. The peripheral distribution he assigns to this nerve fulfils all the conditions of both components. In *Amblystoma punctatum*, HERRICK describes the ophthalmicus profundus as forming into three terminal branches, and mentions the anastomosis with the palatinus VII as a "broad commissure." His figures suggest that he saw the two nerves, the mesal and lateral, derived from this anastomosis, but he has

not shown its real nature. The infra-orbital nerve he calls the maxillaris and assigns it to the trigeminus. He makes this maxillaris homologous with the maxillaris of higher forms.

In *Salamandra maculata*, according to KINGSLEY's correction of the work of VON PLESSSEN and RABINOWICZ, the relations between the nerves in question would seem to be essentially the same as I have described them in *Amblystoma tigrinum*. However, neither VON PLESSSEN and RABINOWICZ nor KINGSLEY describe the compound nature of this anastomosis.

In *Cryptobranchus alleghaniensis* (Menopoma Harl.) FISCHER describes the first branch (ophthalmicus profundus) of the trigeminus as anastomosing, by a branch given off in the region of the muscle rectus superior, with the second branch (maxillaris) of the trigeminus. WILDER confirms this anastomosis and says that the nerve resulting from it anastomoses through a few fibers with the palatinus VII. MCGREGOR, mentioning the anastomosis between the ophthalmic and maxillaris, says nothing of the fibers which enter the palatine. He claims, however, that the presence of lateral line organs ventral of the eye proves the presence of lateral line fibers in the maxillaris (second branch, of FISCHER). If there are such fibers in this nerve it would seem to be homologous with the infra-orbital nerve in *Amblystoma*, in which case the anastomosis with the ophthalmic would present some difficulty. But MCGREGOR does not claim completeness for his work inasmuch as it was mostly done by dissection.

In *Amphiuma*, according to WILDER, the relation between the ophthalmic and maxillaris are the same as in *Cryptobranchus*. He describes also a similar anastomosis between the same nerves in *Siren lacertina*, but none between either the ophthalmic or maxillaris and the palatine.

In *Necturus* MISS PLATT has observed the ontogenetic development of the nerve which corresponds with the infra-orbital nerve in *Amblystoma*. She shows that the nerve consists of general cutaneous V and accustico-lateral VII components which are intimately associated in the process of differentiation from the ectoderm. The general cutaneous component of this nerve

she makes homologous with STRONG's lateral "accessory ramus" of the trigeminus of the tadpole. If, from her standpoint, MISS PLATT can show that the ontogenetic development of the "accessory ramus" and the buccal VII in the tadpole corresponds with that of the two components of the infra-orbital nerve in *Necturus*, the evidence will be most conclusive, but she has offered no exact data to sustain the homology. MISS PLATT's suggestion, however, is the only one I have been able to find in the literature as to the representative in *Urodela* of STRONG's "accessory ramus" in the tadpole.

In *Spelerpes bilineatus* MISS BOWERS says that the ophthalmicus profundus, near the muscle rectus internus, divides into three branches; but her drawings represent the "middle one of the three branches" as coming off of the mesal or "most dorsal." It is impossible to say which representation is correct. The one in the drawing would sustain her homologies better than the one in the text. But from her descriptions generally I am led to believe that the relations are essentially the same in *Spelerpes* as I find in *Amblystoma*. Her diagram of the anastomosis of the ophthalmicus profundus and palatinus indicates that the palatinus divides posterior of the internal nares as it does in *Amblystoma*, each division receiving fibers from the ophthalmicus profundus. If such is the case, the homologies which she proposes for the terminal rami of the ophthalmicus profundus are extremely doubtful.

In her treatment of the infra-orbital nerve in *Spelerpes*, MISS BOWERS distinguishes accustico-lateral and general cutaneous components, considering the latter component as representing the maxillaris V. She observes, however, that this nerve does not anastomose with the palatinus VII as the maxillaris does in *Rana*. In its relation to the buccal VII the general cutaneous portion of this nerve in *Spelerpes* approaches more nearly the conditions found in *Rana* than does that of *Amblystoma*, providing we consider this component as homologous with the "accessory ramus" in the tadpole.

The works reviewed above serve only to show that there are, in the gross structure of different genera of *Urodela*, vari-

ations which, when fully known, may throw light upon the particular points in question. The roots, ganglia and main trunks of the nerves of Amphibia in general have been faithfully dissected, but the finer peripheral relations of these parts demand greater detail in description before any broadly comparative evidence can be deduced upon the questions presented in this paper. The conclusions offered here are, therefore, based wholly upon my own observations and concern only Amblystoma and Rana.

#### CONCLUSIONS.

1. In both Rana and Amblystoma there are two anastomoses in the roof of the mouth between the general cutaneous component of the trigeminus and the communis component of the facial. These anastomoses take place through the palatinus VII which, in both cases, divides, sending one division lateral and the other mesal of the internal nares.

2. The regions innervated respectively by the mesal and lateral branches of the palatinus VII through anastomosis with the general cutaneous component of the trigeminus correspond in the two genera. The branches of the palatinus VII must, therefore, be homologous each to each.

3. The communicating nerve between the palatinus VII and ophthalmicus profundus V in Rana can not be homologous to the communicating nerve between the nerves of the same name in Amblystoma, since the former anastomoses with but one branch of the palatinus VII while the latter communicates with both branches of that nerve.

4. The anastomosis between the general cutaneous component of V and the lateral division of the palatinus VII takes place through the maxillaris nerve in Rana and through the ophthalmicus profundus in Amblystoma. The function of the maxillaris in Rana is therefore performed in Amblystoma by the ophthalmic so far as the oral cavity is concerned.

5. In cutaneous distribution, also, the function of the maxillaris in Rana is performed by the ophthalmic in Ambly-

stoma. The terminal branches of the ophthalmicus profundus in *Rana*, therefore, can not be homologized each to each with the terminal branches of that nerve in *Amblystoma*.

6. As a general conclusion from the above, there is no distinct maxillaris branch of the trigeminus in *Amblystoma*. The functions of that nerve are performed by the ophthalmicus profundus.

7. The general cutaneous branch of the trigeminus associated with the buccal VII in *Amblystoma* corresponds to STRONG's lateral "accessory ramus" in the tadpole.

*Brown University,*  
*April 3, 1901.*

#### DESCRIPTION OF PLATE V.

*Fig. 1.* Projection, upon the horizontal plane, of the rami ophthalmicus profundus V and palatinus VII of *Amblystoma tigrinum*, to show the anastomosis between these nerves.

*Fig. 2.* Projection of the same nerves of the larva of *Rana* together with the ramus maxillaris V, on the horizontal plane (after STRONG), to show the character of anastomoses as compared with that in *Amblystoma*.

*Fig. 3.* Four transverse sections through the head of a tadpole of *Rana*, at a stage some time previous to the appearance of the hind legs. Drawn with the camera lucida to show the relations of nerves at various levels.

*Fig. 4.* Four transverse sections through the head of *Amblystoma tigrinum*, drawn with the camera lucida, to show the relations of nerves as compared with *Fig. 3*.

In *Figs. 3, 4*,

A. Near the anterior end of the Gasserian ganglion, to show especially the relation of *ac* to *m*, *b* and *g*. *Fig. 3A* is immediately cephalad of the Gasserian ganglion.

B. At the level of the passage of *ac*, *b* and *m* around the anterior border of the ear capsule.

C. At the posterior level of the eye.

D. At level of posterior end of internal nares.

#### REFERENCE LETTERS.

*ac.*—Ramus of the trigeminus which fuses with buccalis VII.

*b.*—Ramus buccalis VII.

*c.*—Brain.

*g.*—Gasserian ganglion.

*l.*—Eye.

- ln.*—Ramus lateralis narium of ophthalmicus profundus.
- lp.*—Lateral division of the ramus palatinus VII.
- m.*—Ramus mandibularis V in Amblystoma, maxillo-mandibularis in Rana.
- mn.*—Ramus medialis narium of ophthalmicus profundus V.
- mx.*—Ramus communicans cum N. palatino of maxillaris V.
- mp.*—Mesal division of ramus palatinus VII.
- mv.*—Mesal division of the ventral terminal branch of the ramus ophthalmicus profundus V.
- mx.*—Ramus maxillaris V.
- n.*—Internal nares.
- o.*—Ramus ophthalmicus profundus V.
- ol.*—Lateral terminal branch of the ophthalmicus profundus V.
- om.*—Mesal terminal branch of the ophthalmicus profundus V.
- os.*—Ramus ophthalmicus superficialis VII.
- ov.*—Ventral terminal branch of the ophthalmicus profundus V.
- p.*—Ramus palatinus VII.
- x.*—The nerve formed by anastomosis of *lp* and *ov*.
- y.*—Nerve formed by anastomosis of *mp* and *ov* in Amblystoma and by *mp* and *mx* in Rana.
- z.*—Ear capsule.



## PRELIMINARY REPORT UPON A CASE OF UNILATERAL ATROPHY OF THE CEREBELLUM.

By O. S. STRONG.

The following are some observations made upon the external features of parts of the brain of a child 3 years and 4 months old. Observations upon the other parts, together with the histological findings, accompanied by figures, will be published later. These observations were made in conjunction with one of my students, C. E. DORAN.

The clinical data are rather scanty. The child never learned to walk nor talk, though it would hum airs to itself. It was not deaf.

The most striking feature of the brain, externally, was the almost complete absence of the left hemisphere of the cerebellum; with the exception noted below no part of the left side of the cerebellum extended more than 2 or 2½ cm. to the left of the median line. This was true except a small lobe, apparently in part representing the flocculus, which protruded some 4 cm. to the left of the median line, dorsal to the VIII, IX and X nerves. Some transverse cuts made through the cerebellum showed an absence of the left corpus dentatum. The inferior vermis was apparently, in part at least, present. All of the external surface of the cerebellum appeared normal.

The cause of the atrophy was not entirely clear but it would seem to be most probably due to some old cyst which occupied the space which should have been filled by the left cerebellar hemisphere.

On the ventral aspect, the right olivary body was apparently entirely absent (cuts made through the medulla have shown that a moiety of it is present); the left olivary body was normal. The cranial nerves were apparently normal.

The pons naturally was highly asymmetrical. The transverse fibers, as viewed externally, were normal on the right side but enormously reduced on the left side laterally to the protuberance of the pons caused by the longitudinal tracts and nuclei within,—so much reduced that the V and VII nerves, instead of being separated by the usual mass of transverse pontile fibers, issued from the pons in immediate contiguity to each other. On the other hand, the pons *protruded* much more on the left side, indicating a greater development of the nuclei pontis and longitudinal pontile fibers on that side.

The left crusta was wider than the right.

A dorsal view of the brain stem to a point beyond the third nerve, the cerebellum removed, showed the following: The median line showed here, as well as on the dorsal view, a marked curvature with the convexity toward the left. This may have been due to the position in which the brain, with the cord attached, rested in the jar of formalin but the fact that the brain was well hardened *in situ* by injections of formalin render this less probable.

The left clava was more elongated, extending further cephalad than the right. The same was true of the left cuneus. In the floor of the ventricle, the left ala cinerea extended much (nearly 2 mm.) further cephalad than that on the right. The two trigona hypoglossi were nearly symmetrical; the left eminentia teres was further cephalad than the right. The left trigonum acustici was also further cephalad than the right and appeared to be somewhat less prominent.

It would seem that this asymmetry of the clavae, cunei, alae cinerae and perhaps the trigona acustici is attributable in part or in whole to the unequal pressure exerted upon the medulla in its growth by the unequally developed halves of the cerebellum.

The left corpus restiforme was much smaller than the right. The funiculus separans (RETZIUS) and area plumiformis (RETZIUS) were present on each side. The striae acusticae were not visible. The sides and roof of the ventricle naturally exhibited asymmetrical markings.

The right superior peduncle was much larger than the left. The taeniae pontis were present on both sides but much more prominent on the left, the accessory bundle from the groove between the lingula and velum noted by RETZIUS (das Menschenhirn p. 49) being observed.

The corpora quadrigemina posteriora were asymmetrical, the left being narrower, more prominent and protruding further caudad, its brachium appearing less prominent than that of the right.

The left corpus quadrigeminum superior appeared to be largely lacking. The same external causes which operated to arrest the development of one side of the cerebellum may have also operated in this region.

The aquaeductus SYLVII narrowed funnel-like to a point at the level of the corpora quadrigemina posteriora where it had the diameter of a mere pin-prick.

Observations upon parts anterior to the mid-brain will be published later, but it may be remarked here that there was not apparent the asymmetry of the frontal lobes of the hemispheres which would be expected in such a brain.

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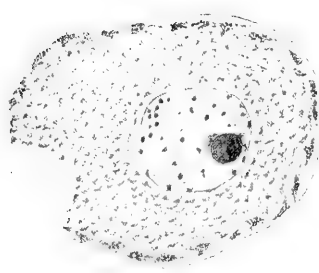


FIG. 2.

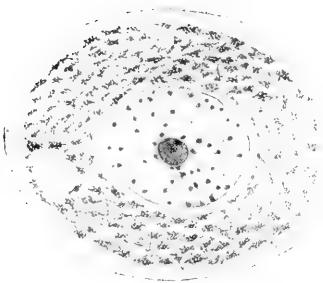


FIG. 1



FIG. 3.



FIG. 4.



FIG. 5.



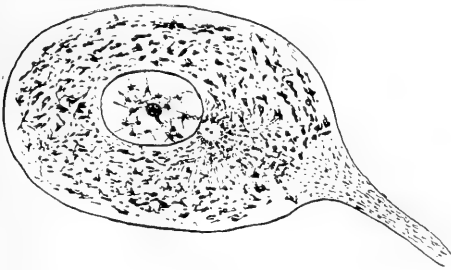


Fig. 1.

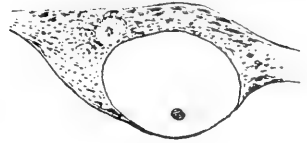


Fig. 4.

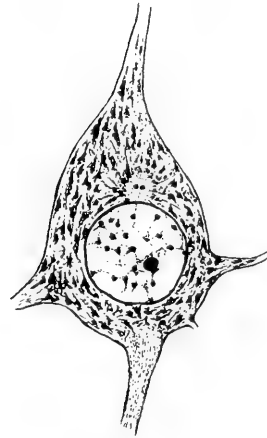


Fig. 2.



Fig. 5.



Fig. 3.



Fig. 8.

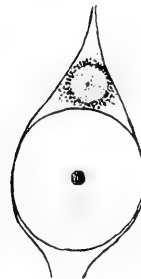


Fig. 7.

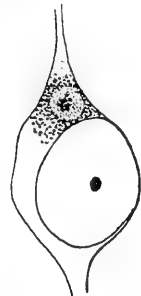


Fig. 6.

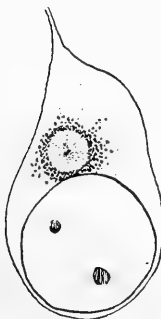


Fig. 9.



Fig. 10.

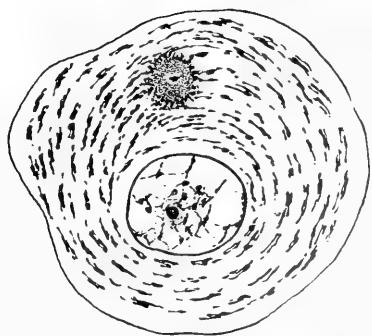
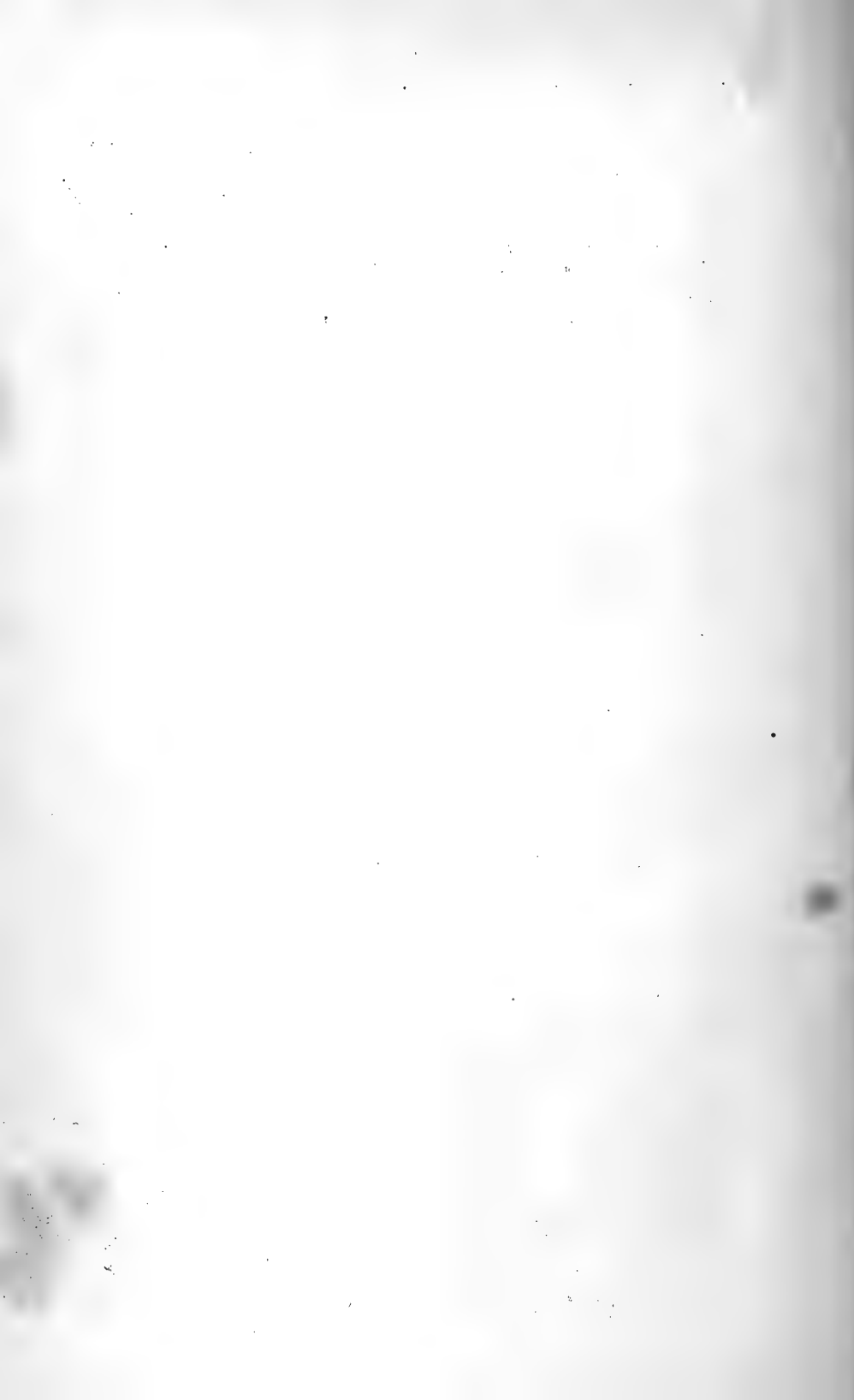


Fig. 11.







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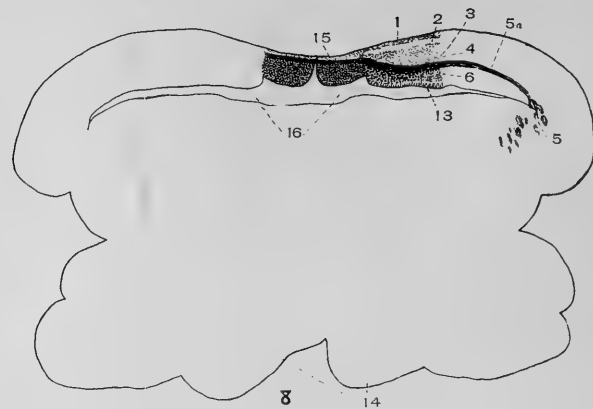
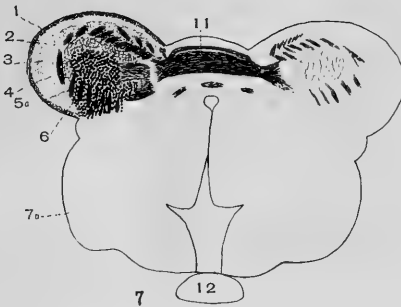
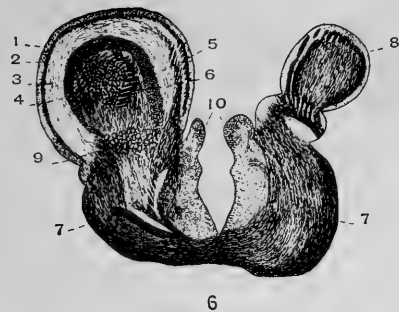
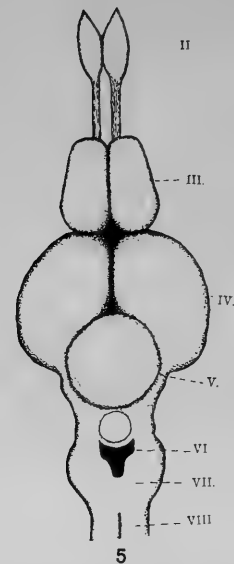
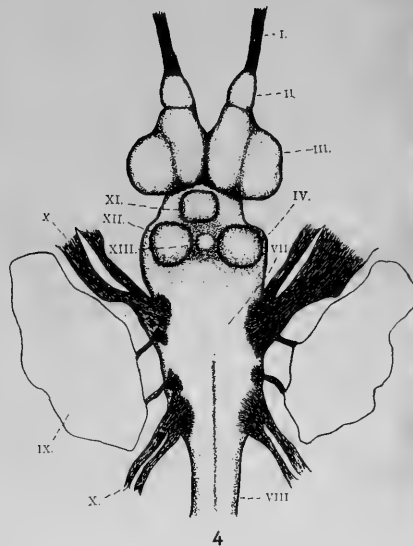
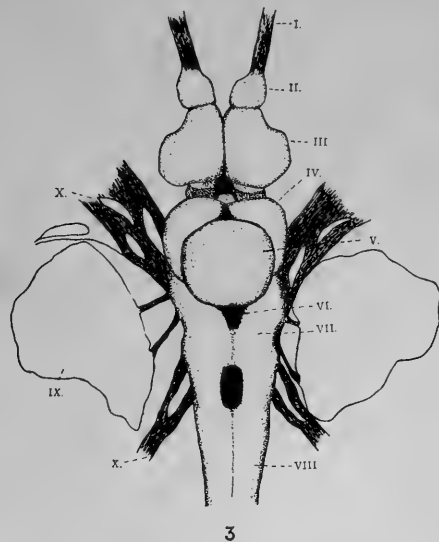




Fig. 1.

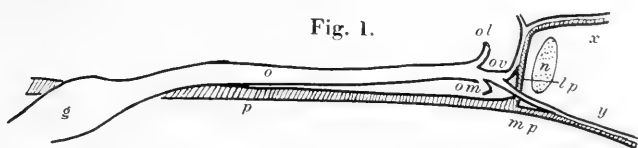


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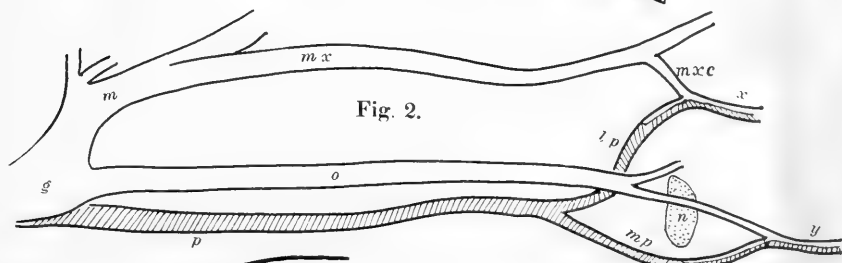
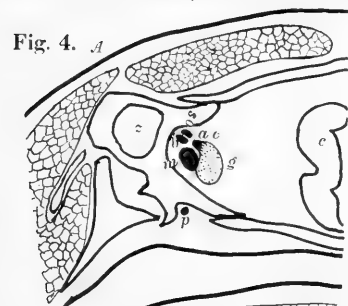
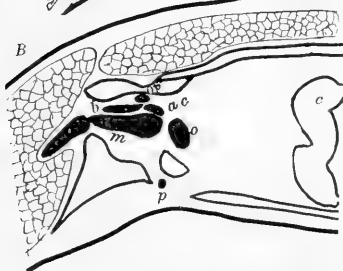


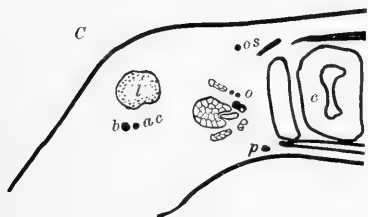
Fig. 4. A



B



C



D

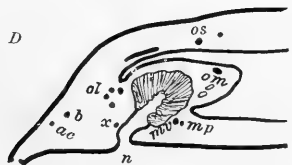
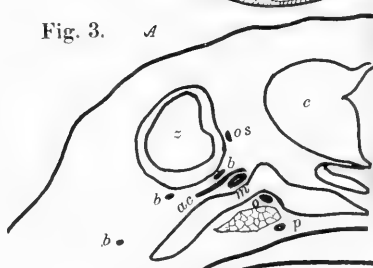
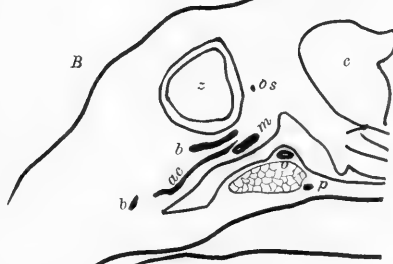


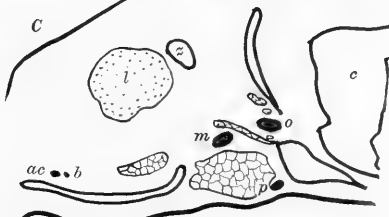
Fig. 3. A



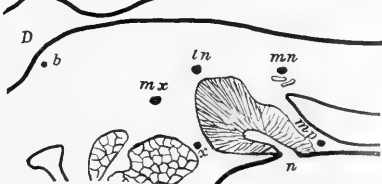
B



C



D





THE

## JOURNAL OF COMPARATIVE NEUROLOGY.

THE NEURONES AND SUPPORTING ELEMENTS OF  
THE BRAIN OF A SELACHIAN.

By GILBERT L. HOUSER,

*Professor of Animal Morphology in the University of Iowa.*

With Plates VI—XIII.

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## SECTION I. INTRODUCTORY.

The student of mammalian neurology has his attention fixed on a mechanism of surpassing complexity. In the pursuit of his work, he is continually touching problems, both morphological and physiological, which frequently transcend all his powers. But the complex nervous skein which he seeks to unravel is merely the final member of a series reaching backward through ever simpler and simpler conditions to the organization of the primitive vertebrate. In other words, the mammalian brain is the product of endless modifications wrought in the original plan of structure by the continual adjustment of nervous mechanisms to the play of a shifting environment. What the architecture of the ancestral vertebrate nervous system may have been we can never hope to know from actual observation. Fortunately, there are simple vertebrates existing to-day which retain many features of primitive nervous organization. To such animals, the student of neurology must ever turn for the solution of the problems which vex him in higher fields. One of these simple vertebrates is represented by a selachian of the modern seas, somewhat specialized in certain directions, of course, but retaining, withal, much of the archaic nervous organization from which higher brains have been gradually evolved. A study of such a simple brain as that of a selachian constitutes, therefore, a necessary introduction to the more highly differentiated nervous systems of birds and mammals.

Our knowledge of the nervous system is so peculiarly de-

pendent upon methods of investigation that the conceptions held by us might almost be said to grow out of the technique employed. The development of neurological methods during the last few years has been indeed phenomenal, and with this advance there has come the necessity for a re-investigation of many nervous systems. The results obtained by the earlier observers, while praiseworthy in themselves, simply do not furnish the precise and complete pictures of neurones which modern comparative neurology requires. And hence it is that the writer has attacked anew the structural problems of a brain which has by no means escaped the attention of investigators. The phylogenetic value usually assigned to the Selachii has caused many to examine the brain of the shark, both anatomically and microscopically. A historical review of the latter class of researches will be found in Section II, 2.

The results set forth in this paper are intended to further exact knowledge concerning the external morphology, the internal organization, and the architectural relations of the selachian neurones, while also aiding, it is hoped, in the elucidation of certain questions of a general character. The particular selachian selected, *Mustelus canis* of DEKAY, is one in which are combined a structure fairly representative of the Selachii as a whole, a size convenient for work, and availability in sufficient numbers to meet the rigorous demands of certain methods of investigation.

This research was begun at the Marine Biological Laboratory of Woods Holl, where two seasons were spent in the use of an abundance of living material. The principal study was continued at the University of Iowa as my regular duties permitted; while certain collateral lines were followed in the neurological laboratory of the University of Chicago. A short preliminary notice of the most important results then in hand was published in the Proceedings of the Iowa Academy of Sciences, Volume IV. The research has finally been brought to completion in the biological laboratory of the Johns Hopkins University.

It is a real pleasure to acknowledge my indebtedness to

the officials of the Marine Biological Laboratory for courtesies extending over a period of several years; and to Professor BROOKS, I cannot do less than express my sincere appreciation of the numerous helpful suggestions given me during the completion of my work.

## SECTION II. REVIEW OF EARLIER RESEARCHES.

### 1. *Anatomical Work Involving Errors of Interpretation.*

To trace the history of a misconception is a task upon which few can enter with even the least degree of enthusiasm, but it is necessary for us to notice briefly here certain erroneous views which have held sway relative to the homologies of the parts of the selachian brain. The interbrain, and along with it the midbrain and often the cerebellum as well, have been variously interpreted by the investigators of the last three decades. MICLUCHO-MACLAY ('70) was the first to break away from the established teachings of VON BAER ('37) concerning the possible homologies of the several brain-segments. Overlooking, in effect, the true interbrain entirely, since he regarded it as nothing more than a longitudinal commissure, MICLUCHO-MACLAY identified the *Zwischenhirn* in that segment which we know as the midbrain; the cerebellum, being next in the longitudinal series, consequently stood for his *Mittelhirn*; while he found his *Hinterhirn* in the small inferior lobe of the true cerebellum. Such an interpretation appears almost inexplicable to us, but we must not allow ourselves to forget that the homologies so confidently traced by us to-day are grounded on many neurological studies, the results of which were not available to the investigators of the earlier period.

Unfortunately for comparative anatomy, the conclusions of MICLUCHO-MACLAY were accepted by GEGENBAUR, and were incorporated by him in the second edition of his *Grundzüge* ('70), and were continued in the smaller *Grundriss* ('74). Appearing also, of course, in the French translation of the former work by VOGT, and in the English translation of the latter by BELL, the errors were, through these several channels, given the

widest possible distribution among investigators, with all the prestige of GEGENBAUR's authority behind them. GEGENBAUR has rectified the mistake in the latest form assumed by his textbook ('98), but it probably will be many years before the mischief is fully undone.

STIEDA ('73b) devoted himself to a correction of the erroneous conceptions promulgated by MICLUCHO-MACLAY and GEGENBAUR. After carefully considering the subject-matter at issue, he embodied his conclusions in a table in which the homologies of the several brain-segments are properly set forth. The work of this author had the effect, at least, of directing the attention of anatomists once more to the fact that the homologies of the fish-brain were really in question, resulting, ultimately, in the true interpretation prevailing at the present time.

ROHON ('77), although writing several years after the publication of STIEDA's paper, did not fully accept the work of that author, but took a position almost between the errors of MICLUCHO-MACLAY on the one hand, and the truth on the other. While giving the cerebellum its proper recognition as a brain-segment, he apparently annexed his *regio ventriculo tertii* to the forebrain, thus leaving the midbrain standing for two whole segments. His *Zwischenhirn*, therefore, embraced the dorsal portion of the optic lobes above, and the hypothalamus below; while he located the *Mittelhirn* between and behind these two divisions of his *Zwischenhirn*. Such an interpretation was certainly remarkable for the ingenuity with which a place was found where an error might be lodged, but it was almost, if not quite, equaled by the general homologies drawn by FRITSCH ('78), who took the whole midbrain for a secondary *Vorderhirn*.

These several errors, curious as some of them certainly are, might have little more than a passing interest for us to-day, were it not that they continue to reappear at intervals, tinging the work of those making claims to a certain degree of authoritative treatment. As an instance of this kind, it may be noted that one of our most recent treatises on comparative anatomy contains a figure of the selachian brain with the cerebellum

designated *lobe optique*, and the anterior end of the oblongata the *cervelet*.<sup>1</sup>

2. *Work on the Microscopical Anatomy of the Brain.*

Anatomical work on the nervous system of the Selachii was begun relatively early, but microscopical study lagged somewhat behind that on the bony fishes. One of the earliest researches touching the microscopical structure of the selachian brain was that of LEYDIG ('52). This versatile investigator was engaged in tracing the general organogeny and histology of the rays and sharks, and so his work upon the brain was not special in its character. Here, however, he discovered the olfactory glomeruli, a result altogether sufficient in itself. Of course, the nature of the microscopical methods then in use did not permit LEYDIG to see much more than the general outline of a glomerulus and the fibres associated therewith. It remained for later workers to trace the full significance of his discovery.

The two decades following the research of LEYDIG witnessed the unfolding of the germ of a special neurological technique. STILLING had introduced the method of studying the brain by means of sections as early as 1842, but the great advantages to be derived from staining the sections were not realized until 1858, when GERLACH soaked his sections in a solution of carmine. Later, 1872, GERLACH obtained such brilliant results with gold chloride as to lead to many trials with this reagent, while some of the possibilities of osmic acid were also becoming known. Finally, chromic acid and the bichromates had come to be recognized as valuable means for hardening nervous tissues. Fortunate that man who was permitted to contribute to the inauguration of a new era in the comparative study of the nervous system, the era of microscopical research. Two investigators extended such a possibility to the field of the selachian brain at practically the same time, VIAULT publishing his results in 1876, and ROHON in 1877.

The research of VIAULT ('76) is quite broad in its scope.

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<sup>1</sup> ROULE, L.: *L'Anatomie Comparée des Animaux*, Tome 2, Fig. 1137. Paris, 1898.

It includes a review of the anatomical features of the selachian nervous system; a description of the structural elements common to all nerve-centres; topographic histology, or the structure of the several parts of the brain and cord; and, finally, a consideration of the homologies of the brain-segments. The figures which accompany the paper are perfectly clear in their execution, but they represent such a low degree of magnification that they are really little more than diagrams. While the observations recorded by this author are of the most general character, he should receive great credit for interpreting the brain-segments properly at a time when there was much confusion in this respect.

In the prosecution of his research, ROHON ('77) had all the stimulating advantages of the laboratory of CLAUS, and his work has a high order of merit. There is a section devoted to the comparative anatomy of the cranial nerves and the several regions of the brain, in both the rays and the sharks. Certain figures illustrating this portion of the work are familiar to all comparative anatomists through their reproduction in the text-books. The histological portion of the research is carefully written, and it is clear that the writer had seen all that the technique of the period would demonstrate. We find in his figures, therefore, nerve-cells represented with some detail of structure, nerve-fibres showing some connection with particular groups of nerve-cells, and fibre-tracts which take a certain definiteness in their courses. The most noteworthy discovery made by ROHON was the *Dachkerne* of the midbrain; see Section VI. But the greatest service which he has rendered consisted in his pointing out for the first time the many structural features which the brain of the selachian has in common with the organization of higher vertebrate brains.

The next research which we have to notice is that of SANDERS ('86). This author seems not to have been familiar with the great advances just made in methods of research, (see *infra*); and so we find him rejecting carmine as a staining medium and expressing a preference for rosaniline because of the clearness of the pictures yielded by it, while he gives a mere hint of

haematoxylin. The scale of the work is ambitious to a degree bordering on superficial treatment. There are to be included the anatomy and histology of the brain, spinal cord, and cranial nerves in both the rays and the sharks. The histological descriptions usually embrace the general distribution of the nerve-cells of a given region, followed by exhaustive measurements of their sizes. His figures are hardly more than outlines of brain-sections, exhibiting very little detail. His most grievous mistake lay in his refusal to apply the brilliant generalization on the pallium which RABL-RÜCKHARD ('83) had published shortly before, rejecting it as an impossible explanation of the selachian forebrain.

We now turn to the work of an investigator whose privilege it has been to lay many of the stones for the foundation of comparative neurology. Dr. EDINGER has demonstrated that it is possible to carry on research in the right way in spite of the exhausting cares of a physician's life. His earlier work ('88) includes the consideration of both the embryonic and adult selachian forebrain as a part of a systematic study of the forebrain of the several groups of vertebrates. By this time there had been given to neurological workers two of the most important methods of investigation yet imagined, the chrome-silver impregnation of GOLGI, and the myelin stain of WEIGERT. The former has led, ultimately, to the modern conception of the neurone as a structural and physiological unit; while the latter, including here the various modifications of the essential principle, has grounded our knowledge of the course of nerve-fibres in the cerebrospinal axis. In the research under consideration ('88), EDINGER was the first to apply the staining method of WEIGERT to the brain of the selachian. Using a counter-stain to define the nerve-cells more clearly, his results were characterized by a precision not known to the earlier workers. The chief part of the text is occupied by a description of the fibre-tracts, and the drawings are evidently intended to illustrate this phase of the subject alone. The nerve-cells are described as to distribution and general external morphology, so far as they are made visible by the method employed.

The principal aim of the research is an elucidation of fibre-tracts rather than the investigation of nerve-cells.

In a later research ('92), EDINGER applied essentially the same methods to the interbrain of selachians and amphibians, and the results have a scope similar to those just noticed for the forebrain. In the later editions of his text-book (1900), he has amplified for the comparative portion of the work the results of all his own studies, together with those of others, giving us the broadest exposition of modern comparative neurology yet attempted by any writer.

To SAUERBECK ('96) belongs the credit of first publishing results from the application of chrome-silver impregnation to the selachian brain. The paper contains a very brief description of those neurones and supporting elements which had been impregnated; by far the greater number of structures present evidently were not demonstrated at all. The treatment is quite unequal for the several regions, and the figures are drawn on a small scale. While SAUERBECK must not be given credit for the things he neither described nor portrayed, yet a first attempt in this field is certainly to be commended.

SCHAPER ('98), in the course of a series of studies on the cerebellum of vertebrates, has taken occasion to apply the chrome-silver method to the selachian cerebellum. His paper records observations with a considerable degree of detail. Reference to the results of SCHAPER will be made more particularly under Section V.

Inspired by the elaborate classification of nerve-cells in general promulgated by NISSL in his writings, SZCZAWINSKA ('98) was impelled to make a study of the internal structure of the selachian nerve-cell. His work presents the results of his researches upon certain types of cells through the use of methylen-blue, safranin, and haematoxylin stains. The cells studied were from the sensory ganglia, motor cells from the cord and oblongata, and cells of PURKINJE from the cerebellum. SZCZAWINSKA reached the conclusion that the nerve-cells of selachians have remained on a low plane of development. In support of this view he cites certain of his results—(1) that the



cell-bodies are usually bi-polar in form; (2) that there is but slight demarcation between the cell-body and its protoplasmic processes; and (3) that the chromophile substance is less differentiated than in teleosts and higher vertebrates.

### SECTION III. METHODS OF INVESTIGATION.

The technique employed in the course of this research has covered a wide range. In fact, every process holding any promise of value has been given a careful trial. It seems desirable to describe here, however, only those methods which have contributed most largely to the final results.

#### 1. *Chrome-Silver Impregnation.*

The production of a chrome-silver deposit in nervous elements is far more than a simple chemical reaction between the potassium bichromate and the silver nitrate employed. There is to be added as a prime factor, the chemistry of the nervous tissues themselves. The substances present in the nervous elements enter into the reaction to such a degree that the results are either positive or negative according to the character of those substances. In the economy of the animal, serving both as the basis for nervous activity and produced as the result of it, there is a constant round of metabolic change altering the chemical composition of the nervous tissues. In my work upon *Mustelus*, it was soon found that strict account had to be taken of the physiological state of the animal. An individual fresh from the pursuit of his prey in the open sea gave altogether different results from one which had been kept for some time in a small aquarium, simply because the reactions of the tissues in the two instances were quite different. And so, before even fair results with chrome-silver impregnation could be secured, it was necessary to make a careful study of physiological conditions.

It was also found that selachian nervous elements lend themselves but grudgingly, at best, to the reaction desired. Numerous trials were made of the several published schemes for securing impregnation, but particularly of the procedure

indicated by GOLGI ('94); by RAMÓN Y CAJAL ('94); by FLECHSIG ('89); by COX ('91); and by STRONG ('95, '96). Every application practicable was also made of formaldehyde as a constituent of the reagents employed. A general critique of these processes has already been given by me in a former paper ('97a).

The slices of perfectly fresh brain from the most active animal procurable were placed in the "rapid" hardening mixture of GOLGI. The pieces were always small, not over two millimeters in thickness for, *e. g.*, a transverse section of the forebrain. The proportion of the hardening fluid used embraced one part of 1% osmic acid to four parts 3.5% potassium bichromate, and this reagent was used in liberal quantities. The proper duration of hardening was influenced by the temperature of the room and the physiological state of the animal, but an average length of time was three days. The greatest clearness of impregnation was secured with silver nitrate solution of 0.75% strength. In the preparation of serial sections, the most desirable clearing agent was found in a mixture of oil bergamot, oil cedar-wood, and melted carbolic acid crystals, equal parts. After being hardened in chloroform, the celloidin blocks were placed in the clearing mixture, and they were kept flooded with the oil during cutting. The above mixture clears the block rapidly, it may be used repeatedly, and it has the additional advantage of allowing the preparations to be kept in it for some time without impairing the impregnation. The sections were cut 75 micra in thickness.

## 2. *The Application of Methylen-Blue.*

Methylen-blue holds so many possibilities as a neurological reagent that we are doubtless but crossing the threshold of its use to-day. I have applied this aniline in every way of which I could learn, and the most important results are set forth below.

a. *The Staining Method of Nissl.*—NISSL's description of his method ('94) called for the fixation of the tissues with alcohol. This has proven an unsatisfactory part of the technique for my work. Better cytological preservation by far has been

secured through the use of the chrome-oxalic mixture of GRAF ('98). This reagent appears to have escaped the general attention of microscopists, at least no mention is made of it in the fifth edition of LEE (1900). The composition is here given :

Oxalic acid, 8% aq. sol. . . . .	200 c.c.
95% alcohol . . . . .	150 c.c.
Chromic acid, 1% aq. sol. . . . .	150 c.c.
Mix in the order as named.	

Quite small pieces of the brain were fixed in this fluid for six hours, and the fixing agent was then washed out with 70% alcohol. Sections were made by the paraffin method.

The slide was taken from distilled water, and the steaming-hot stain of NISSL was poured over the sections, five minutes. The excess stain was rinsed away with distilled water for the briefest possible time, and the water clinging to the slide was absorbed with filter paper. Differentiation with the anilin-alcohol of NISSL took but a few seconds, being stopped by flooding with oil of cajeput just as soon as the sections took on a delicate rose tint. Clearing with the oil of cajeput was aided by holding the slide for a few moments in gentle heat. Mounting was done in colophonium dissolved in xylol. The staining is remarkably precise, and the color has shown no tendency to fade.

The counter-staining methods described by HELD ('95), and by WARRINGTON ('98), were also applied, with certain modifications found necessary. The erythrosin mixture of HELD was gently warmed, poured over the slide for ten seconds, and then washed away quite thoroughly with distilled water. Staining was done with either the pure stain of NISSL, or with the same diluted with an equal volume of 5% acetone; the results did not seem to differ very much. In either case, the stain was heated and allowed to act for five minutes. Differentiation with 0.1% alum solution for just a few seconds, until the sections appeared distinctly red, was followed by a brief rinsing with water. The results given by this process have been of value as an accessory to the pure methylen-blue stain, but they are far from supplanting the original method.

*b. Intra-Vitam Injection.*—The coloration of the nerve-cells through intra-vitam injection of methylen-blue was given a most thorough trial, a large number of animals being utilized for this purpose. The subcutaneous injection preferred by MEYER ('96) is not practicable for *Mustelus* because of the absence of either loose areolar tissue or of lymph spaces. The syringe was therefore inserted directly into the vascular system. A 5% solution of methylen-blue, BX brand, was injected some four times during the course of an hour. Beginning with a small quantity, the amount rose successively until as much as 30 c.c. was introduced in the final injection, making some 50 c.c. in all. This whole process was governed, however, not by fixed quantities of the reagent nor by exact periods of time, but by the stopping of the heart's action and the blueness of the animal. Half an hour after the final injection, the brain was removed, cut into thin slices, and then exposed to the air until the tint had become a brighter blue. In the conversion of the unstable methylen-blue stain of the fresh tissues into the insoluble form, I have not been successful with the method recommended by BETHE ('96). The use of the picrate of ammonia as a preliminary fixer has seemed to actually impair the clearness of the final preparation. I obtained the best results with the solution given by MEYER ('96):

Distilled water	. . .	100 c.c.
Ammonium molybdate	. . .	10 grams
Hydrochloric acid	. . .	10 drops

Heat the first two ingredients together, then add the acid.

The pieces of brain were placed in this mixture, cooled with ice, for four hours. They were then washed with iced water for two hours. Dehydration with cooled alcohols, and imbedding in paraffin were hastened as much as practicable; in fact, it is well to have the tissues in paraffin on the same day when the injection was begun. The preparations were used chiefly for the study of the architectural relations between the neurones, and so the sections were cut quite thick.

The results given by this method are characterized by exceptional clearness, due, in large measure, to the selective col-

oration of certain neurones, only. The attainment of the desired end is far from constant, however. After experience had shown the rule, care was always taken to apply this technique only to those animals which had been in an active condition, fresh from the open sea, if possible. But even with this precautionary recognition of physiological conditions, so far as they could be readily determined, there apparently yet remained some unknown factor which caused a negative result in some instances where it was least expected.

### 3. *Iron Haematoxylin.*

This reagent was imagined by HEIDENHAIN ('92) for refined cytological work, but it truly has a place in neurological investigation. It is a most excellent stain for defining the internal structure of the nerve-cell, and also for the tracing of nerve-fibres. For the latter purpose, iron haematoxylin has proven itself preferable in this research to the stain of WEIGERT, since it defines the axis-cylinder instead of the myelin, permitting fibres to be followed through their ramifications entirely to the terminal arborizations.

Fixation of the tissue may be done with any good fluid. Where the tracing of axones, only, is desired, 10% formaldehyde cannot be surpassed; but where the aim is purely cytological, either the chrome-oxalic mixture of GRAF or the fluid of FLEMMING will give superior results. For work on axis-cylinders, celloidin sections were made 30 micra thick; and for the minute study of the nerve-cell, thin sections were cut by the paraffin method.

The sections were brought from distilled water into the mordant of 4% iron alum for two hours. The excess mordant was then rinsed away with distilled water. Staining with 0.5% aqueous haematoxylin required at least four hours for entirely satisfactory definition. Clean tap-water was used for washing out the uncombined stain, since this appears to fix the lake more firmly. The stain was differentiated with a 2% solution of iron alum, frequently renewed. This process was observed with the microscope, and when the desired effect had been ob-

tained, the sections were transferred to tap-water. Thorough washing at this stage is necessary to prevent fading of the stain, and the slight alkalinity of ordinary tap-water appears to be a factor aiding in its preservation.

#### 4. *The Chloride of Vanadium Method.*

The technique required for staining with the chloride of vanadium method of WOLTERS ('90) is somewhat troublesome, but the results, when obtained, certainly justify the means. Nerve-cells, axis-cylinders, ependyma, and neuroglia are all defined in one and the same section. No other method known to me gives so comprehensive a picture for general study. Its sole value lies, however, in the purely general scope of the results.

It is hardly necessary to give a description of the process here, since its essentials are outlined in LEE (1900, p. 410).

### SECTION IV. THE OBLONGATA.

#### 1. *General Morphology of the Oblongata.*

In *Mustelus*, the transition of the architecture of the spinal cord into that of the oblongata is traceable with a degree of definiteness which rarely obtains in other animals. It is therefore possible to contribute toward the solution of certain problems which vex the study of this highly specialized region of the mammalian brain. Only an introductory survey of the entire field will be presented here, leaving the development of details and the consideration of special questions to the following subsections.

As the *canalis centralis* widens into the fourth ventricle, the several structures of the cord lateral to it are pushed into more and more widely divergent positions, retaining, however, essentially the same mutual relations to each other. Concomitant with this divergence, the dorsal ependyma becomes broadened to form the morphological roof of the fourth ventricle (Fig. 2, *t. c. p.*).

In approaching the oblongata, the ventral cornua are encroached upon more and more by commissural fibres until, just above the level of the first spinal nerve, the mammalian hypo-

glossus, these nuclei disappear altogether as continuous collections of nerve-cells. A small number remain associated as the nucleus of the abducens, while the remaining neurones become scattered through the formatio reticularis (Fig. 2, *c. n.* and *t. n.*).

The intermediate zone and the dorsal cornu of the cord are relatively small in size, but as the paired halves diverge to right and left of the fourth ventricle they increase in mass and assume characters and functions of a special order for each region. The intermediate gray matter contributes the lobus vagi and the visceromotor nucleus of the oblongata; while the dorsal cornu becomes specialized as the general cutaneous nucleus. We will note each of these in turn.

The lobus vagi is a longitudinal elevation in the lateral wall of the fourth ventricle (Fig. 1, *l. vg.*). Anatomically, it is one of the most striking features of the oblongata because of the row of bead-like prominences into which its surface is thrown. The position of the structure as seen in a transverse section is represented in Fig. 2, *l. vg.* The lobus vagi is the terminal station for communis components of the VII, IX, and X nerves; see Subsection 4. Certain of these fibres, instead of passing directly to their termination here, enter a compact bundle and run posteriorly to the spinal cord. This tract is known as the fasciculus communis. Its position in the oblongata will be seen in Fig. 2, *f. c.*

The visceromotor nucleus is a column of large nerve-cells imbedded in the lateral wall of the fourth ventricle (Fig. 2, *v. m. n.*). Different portions of this column are known as the nucleus ambiguus, and the motor nuclei of the VII and V, respectively. The axones for the motor roots of the V, VII, IX, and X nerves take their origin from these nerve-cells. It is a curious fact, however, that but few of the axones pass directly into their nerve-roots, but take a course first in the fasciculus longitudinalis dorsalis. This is a massive, paired tract, the two bundles lying side by side beneath the floor of the fourth ventricle (Fig. 2, *f. l. d.*). There are present in the dorsal longitudinal bundle nerve-fibers from several sources. Into this crowded highway the axones from the visceromotor nucleus

penetrate, to finally emerge as the motor roots of their respective nerves.

The dorsal cornu of the cord is continued into the oblongata in an enlarged condition, and it becomes associated with sensory fibres of the V, IX, and X nerves to form the general cutaneous nucleus (Fig. 2, *g. c. n.*). The neurones of this nucleus provide a primary termination for certain general cutaneous fibres; while others turn backward to the cord as the spinal V. tract. At the posterior levels of the oblongata this system appears dorsal to all other structural features, the pair forming the rounded, crest-like margins to the fourth ventricle. Proceeding anteriorly, the nucleus is pushed into a position both more ventral and more lateral by the superposition of a new structure, the tuberculum acusticum.

The tuberculum acusticum is shown in Figs. 1 and 2, *t. a.* It extends posteriorly from the restiformis along the lateral margin of the fourth ventricle some three quarters of the distance to the calamus scriptorius, tapering as it proceeds. It is separated from the general cutaneous nucleus below it by a fissure which reaches well toward the limitans interna. The outer zone of the acusticum is structurally continuous with the cerebellum; it is known as the cerebellar crest (Fig. 2, *cb. cr.*). The acusticum is the centre for the nerves of the lateral line sense-organs and the internal ear. Its interpretation will be considered in Subsection 7.

## 2. *Review of Nerve Components.*

A proper point of view for the structure of the oblongata can best be obtained through familiarity with the problems of the cranial nerves pertaining to this region of the brain. Reference to the text-books of descriptive anatomy will discover hardly a trace of the conceptions which dominate the modern morphology of nerves. The discovery made by SIR CHARLES BELL as to the character of the dorsal and ventral roots of the spinal nerves was one which represented a distinct advance in sound physiology, but the application of BELL's formula to the cranial nerves has not been productive of sound morphology.



The effort to compare the cranial with the spinal nerves on the simple basis of "sensory" and "motor" could not avoid leading to many dogmatic positions concerning the real character and ultimate distribution of many fibres. An attempt to solve such intricate problems through so mechanical a method could hardly be otherwise than faulty, particularly when applied to the specialized conditions of the mammalian nerves. A thorough study of the less modified cranial nerves of the Ichthyopsida is a necessary preparation for sound morphological work in the higher field.

The views of cranial nerves held by the neurologists of to-day were founded less than a decade since, but the germ of the central idea is traceable to a somewhat earlier date. GASKELL in a series of publications ('86, '88, '89) was making the attempt to solve the metamerism of the head and the origin of the vertebrate nervous system through a study of the nerves. He took occasion to show that a spinal nerve not only embraces the sensory and motor fibres of BELL, but that its structure, distribution, and function, as well as the arrangement of its central nuclei, lead to the divisibility of the nerve into two parts. One part is somatic, innervating the external surface of the body, and the muscles derived from the muscle-plates. The other division is splanchnic, supplying the internal organs and surfaces, and those muscles which GASKELL characterizes as "derived from the lateral plates of the mesoblast." GASKELL attempted to show, further, that the cranial nerves arise from centres homologous with the spinal centres, likewise divisible into somatic and splanchnic groups.

The impetus given by GASKELL has led, ultimately, to the modern conception that a spinal nerve embraces neurones derived from four distinct sources, with as many different distributions. There are, then, to be distinguished in a spinal nerve : (a) Somatic motor fibres. These neurones have their cell-bodies situated in the ventral cornu of the cord, their axones emerge through the ventral root, and they are distributed to the body musculature. (b) Somatic sensory neurones, the cell-bodies of which comprise the dorsal ganglion, and their fibres connect

peripheral end-organs with the dorsal cornu of the cord through the medium of the dorsal root. These two divisions of a spinal nerve comprise the principal number of fibres in the two roots. (c) Viscero-motor; these fibres take their origin from a group of cells, the paracentral nucleus of ONUF and COLLINS ('98), lying lateral to the canalis centralis; they emerge through both the ventral and the dorsal roots, and are distributed to the non-striated muscles of the viscera. (d) Viscero-sensory neurones, from the viscera, through the dorsal root, to termination in the intermediate zone of the gray matter.

A new era in the investigation of cranial nerves was inaugurated by STRONG ('95) when he made the application of these principles to larval amphibians. STRONG found that it is practicable to recognize certain distinct classes of fibres or components of the cranial nerves, which are to be distinguished from each other by their size and histological characters, by their central origin or connections, and by their ultimate distribution. KINGSBURY ('97) made a careful extension of these findings to several ganoids and teleosts; while HERRICK ('97, '98, '99) has traced the conditions in the bony fish, *Menidia*, with admirable clearness. Certain conclusions reached by JOHNSTON ('98b) from his study of the ganoid brain stand apart from the general trend of recent work, and to these we shall return further on.

The principles developed by the researches of STRONG, KINGSBURY, and HERRICK, may now be applied to the cranial nerves of *Mustelus*. There are to be distinguished five systems of nerve components:

*a. The Somatic Motor System.*—This system of neurones is homologous with the ventral-cornu neurones of the spinal cord. The fibres take origin from cells having a ventral location in the brain, and they innervate striated somatic muscles. The only representatives of this class are the nerves of the eye-muscles, the III, IV, and VI, respectively.

*b. The General Cutaneous System* is so-called because concerned with the innervation of the skin of the head, but it is not associated with specialized peripheral sense-organs of any kind. Its fibres are components of the V, IX, and X nerves,

and they are homologous with the somatic sensory spinal fibres. The cell-bodies of these neurones lie in sensory ganglia, and the central termination is comparable to that of the somatic sensory spinal fibres. Part of the general cutaneous fibres terminate in the general cutaneous nucleus, the homologue in the head of the dorsal cornu; see Subsection 6; but others turn into the spinal V tract and take a course posteriorly for ultimate termination in the dorsal cornu of the cord. There can be no question as to the identity of this system with the somatic sensory system in its simpler condition.

*c. The Viscero-Motor System.*—Fibres of this system form the motor roots of the V, VII, IX, and X nerves. The cell-bodies from which the axones arise form a column of cells lateral to the fourth ventricle, known, according to the level, as the nucleus ambiguus, and the motor nuclei of the VII and V, respectively. This column of cells is the cranial continuation of the paracentral nucleus of the cord, and the homology is rendered complete by the distribution of the fibres to the visceral musculature.

*d. The Communis System.*—This term is used in the sense defined by HERRICK ('99, p. 208), and as the equivalent of the fasciculus communis of STRONG ('95) as applied to the system in the tadpole, and of KINGSBURY ('97) as used for various fishes. Communis fibres are components of the VII, IX, and X nerves. They are wholly sensory. They innervate visceral and mucous surfaces; and also taste-buds and those specialized sense-organs of the skin (end-buds) not referable to the lateral line system. The fibres are characterized by their small size, and they are distinguishable from other components of the same nerves by this feature. They terminate in the lobus vagi. The greater number of them in *Mustelus* pass directly to their central termination without entering the fasciculus communis, using this term in the sense as originally applied by OSBORN ('88) to a definite longitudinal tract.

The communis system is homologous with the viscero-sensory system, the lobus vagi in which its central termination occurs being the continuation into the brain of the lateral or interme-

diate zone of gray matter in the cord. The viscerosensory system in its original condition is, however, of far less importance than its cranial representative. The communis system not only innervates visceral organs, but it has come into relations with taste-buds and peripheral end-buds, as well. It therefore is a system having a very considerable magnitude.

*e. The Acustico-Lateral System* is concerned exclusively with the innervation of the internal ear and the organs of the lateral line. Its fibres are components of the VII, VIII, and X nerves. They penetrate the tuberculum acusticum for immediate termination there or for a course farther forward into the cerebellum. The significance of the latter termination will be discussed later. The components of this system in the VII and X are to be readily distinguished from other fibres associated with them by virtue of their great diameter.

The acustico-lateral system is not represented in the spinal nerves, as the four preceding cranial systems are. The evolution of this system is bound up with that of the peculiar series of sense-organs which it supplies. Until the evidence is more nearly complete as to the embryology and affinities of the lateral line and its nerves as a whole, we really are not warranted in making any positive assertion as to its phylogeny. Some evidence as to the possible origin of its centre will be given in Subsection 7.

### 3. *Neurones of the Ventral Cornu.*

Upon reaching the level of the oblongata, the ventral cornua of the cord become broken up as distinct collections of nervous matter. Somatic motor neurones from this source are grouped into the nucleus for the VI nerve, but elsewhere there are only isolated individuals lying between the fibres of the *formatio reticularis*. In an earlier paper touching this subject ('97b), I left the interpretation of these scattered neurones undecided. It is now certain that they correspond to the commissural cells and the tract-cells (*Vorderstrangzellen*), respectively, which VON LENHOSSÉK ('94) has described from the spinal cord of the selachian.

*a. Tract-Neurones.*—The ventral tract-neurones are scattered over the mid-ventral field of the oblongata on each side of the raphe ventral to the dorsal longitudinal bundles (Fig. 2, *t. n.*). They are to be readily distinguished from all other neurones of this region by their size, for they are really giants. Their size is exceeded only by the neurones of the midbrain roof-nucleus described in Section VI, Subsection 2.

As to external form, the tract-neurones have a wide range; a representative individual is drawn in Fig. 2, *t. n.* There are from three to five dendrites, and their disposition controls the shape of the cell-body to a very high degree. The dendrites may be given off at opposite extremities of the cell, in which case the outline of the cell-body is a much elongated one. The form is rounded or stellate when the dendrites are spaced at equal intervals. A dendrite is always a massive process, very wide at its base, tapering quite gradually, and reaching far out into the surrounding nervous matter. It gives origin to but few branches.

The axone always arises from the body of the cell. It runs for a short distance in the transverse plane and then turns into a longitudinal bundle of fibres on the same side of the oblongata, or even on the opposite side.

The internal organization of a tract neurone is shown in Fig. 44. The cytoplasm is voluminous in quantity, investing the nucleus with a thick layer on every side. The outline of the nucleus is regular, and in form may be circular or oval. There are always a remarkably small number of coarse chromatin granules, the chromatic material being distributed in the form of a delicate reticulum. Subsidiary nucleoli are rarely present.

The cytoplasm is, as already noted, great as to actual quantity. Some neurones when stained by the method of NISSL absorb the methylen-blue equally throughout all parts of the cytoplasm, and hence they appear almost homogeneous; the significance of this fact is noted below. Other neurones in the same section exhibit a large quantity of tigroid substance; the neurone represented in Fig. 44 is of this type. In the vicinity

of the nucleus the tigroid-bodies are usually triangular in outline, and some of them have a very considerable size. Tigroids are found far out in the dendrites, assuming here a lenticular or even a linear form, their long axes parallel with the course of the dendrite. A finely granular axone-hillock lies at the origin of the axone. In rectangular cells, as the one figured, the hillock may be spread so widely as to assume a disk-like form. The tigroids tend to become somewhat smaller in the region of the hillock.

The tract-neurones are not demonstrated readily with either chrome-silver impregnation or the intra-vitam injection of methylen-blue. The homogeneous coloration assumed by some of them with NISSL staining has already been recorded. The character of such micro-chemical reactions indicates clearly that many of these neurones are not physiologically active, at least not all of the time. The axones from some of them may enter the motor root of one of the anterior spinal nerves, and, being in an active condition, give indications of it in a well-marked store of tigroid substance. Other neurones, however, chaining together higher and lower levels of the oblongata, have come to have their functions largely usurped by the development of more specialized tracts. Such neurones are, therefore, degraded to a far lower plane of metabolic activity, and they respond but feebly to those of our stains which depend upon the presence of definite chemical constituents of the protoplasm.

*b. Commissural Neurones.*—The commissural neurones are readily distinguishable from the tract-neurones by their smaller size (Fig. 2, *c. n.*). Commissural neurones have a wide distribution. They are scattered between the tract-neurones in the vicinity of the median raphe, and they also are to be found in all parts of the lateral region as far dorsal as the base of the general cutaneous nucleus.

The external morphology of a commissural neurone is represented in Fig. 3, *c. n.* The cell-body is relatively small in proportion to the extension of the dendrites and the axone. The form of the cell is usually an elongated oval or an irregular triangle. The dendrites are quite often only two in num-

ber, arising from the ends of the cell. The course taken by the dendrites does not seem to be affected in the least by the tracts of fibres of the formatio reticularis, since it frequently takes them obliquely through a bundle of arcuate fibres. The dendrites are stout at their bases. They give off only a few branches. The principal axis of the dendrite pursues a rather even course for a comparatively long distance, tapering gradually to the end. Its surface bears but few gemmules.

The axone may arise from the body of the cell, or, when the long axis of the cell is horizontal, from one of the dendrites. It takes a course directly for the opposite side of the oblongata, giving off collaterals near its point of origin and then remaining free from them. The function of such an axone is, doubtless, commissural.

The internal structure of a commissural neurone from the right side of the oblongata is drawn in Fig. 45. The cytoplasm is always far less voluminous in proportion to the size of the nucleus than in the tract-neurones. The nucleus is almost invariably oval in outline, with its major axis disposed the long way of the cell. The nucleolus is not conspicuous. The chromatic material is distributed in elongated, irregularly formed strands which lie throughout all parts of the nucleus. The several masses may be connected with each other, but only the faintest suggestion of it is indicated with the highest magnification.

The cytoplasm contains a considerable quantity of tigroid substance. A few broadly triangular tigroids are scattered round the nucleus, sometimes in the condition of nuclear caps. The greater part of the tigroid substance is to be found at the wide expanse where the cell-body merges into a dendrite. Here the form of tigroid is a greatly elongated triangle. This is replaced farther along the dendrite by spindle-shaped or linear masses. A small axone-hillock of finely granular matter lies just within the origin of the axone. The tigroid-bodies near it are smaller and more irregular than elsewhere.

The commissural neurones, in contrast with the tract-neurones, always respond to the stains applied; this indicates a

uniformly active physiological condition. Commissural neurones doubtless have a not unimportant place in the economy of this region of the brain, into which so many impulses sweep through afferent nerve-fibres to great vital centres. The chaining together of the opposite halves is precisely what we should expect to find under such conditions, and the mechanism is provided by the commissural neurones just described.

#### 4. *Lobus Vagi and Fasciculus Communis.*

The lobus vagi is the terminal station for the communis fibres, components of the VII, IX, and X nerves. Its general morphology has been outlined in Subsection 1.

The structure of the lobus vagi embraces a narrow zone next to the limitans interna occupied chiefly by nerve-fibres; and a deeper part in which there are both neurones and terminating fibres. The course of the nerve-fibres will be considered later.

a. *Neurones of the Lobus Vagi.*—The constituent neurones of the lobus vagi are many in number and closely crowded. They are comparatively small in size, and are referable to type II of GOLGI. The external morphology of a neurone is shown in Fig. 4.

The shape of the cell-body ranges from almost triangular to broadly oval. The axone may emerge directly from the cell-body, or it may spring from one of the larger dendrites. It pursues an irregular course away from the limitans interna into the deeper levels of nervous matter. Before proceeding far, it breaks up into a widely-spread arborization such as is characteristic for neurones of this type. I believe, from the course of the axones, that they constitute a means for transmitting impressions to the visceromotor nucleus; see Subsection 5.

The dendrites are three or four in number. They are quite stout near their origin, they taper gradually, and they do not become very fine at their terminations. Their morphology is simple, since there are only one or two branchings at most. Their lengths may be as great as that of the axone, and so the dendrites from all of the neurones here interlace to form a veri-



table jungle. The surface of a dendrite bears a few gemmules, together with certain small knobs and elevations of various shapes.

The internal organization of a neurone from the right lobus vagi is shown in Fig. 46. The nucleus is always large in proportion to the bulk of the cell. In some instances there is only a thin film of cytoplasm enclosing it at certain points. The nucleus is a more or less perfect oval, holding one or more nucleoli. The chromatin is distributed in a few thin, branching strands which give the appearance of joining in some parts of the nucleus. The chromatin never stains intensely in these neurones, and so the nucleus is represented by light coloration in the figure.

The cytoplasm lies principally in the broad areas where the cell-body merges into the dendrites. Its tigroid substance is never collected into large masses. In the region of the nucleus, the tigroid material is chiefly in the condition of medium-sized granules, with a few small triangles intercalated. The dendrites have fusiform or linear tigroids scattered at irregular intervals. A very small axone-hillock gives origin to the axone. In the specimen figured, this lies at the side of the most massive dendrite, but this location is not the rule for these neurones.

*b. Termination of Communis Fibres.*—By far the greater number of the communis fibres from the VII, IX, and X nerves pass directly to their termination in the lobus vagi, a few, only, entering the fasciculus communis, described below.

Fibres penetrate the lobus vagi for ultimate termination chiefly from the dorsal side (Fig. 2, *c. f.*). They reach this position by a sweeping curve which carries them to an ever higher level as they run inward from the exterior. These incoming fibres constitute a thin stratum next the limitans interna, the neurones lying just beneath. The final arborization occurs near the body of some neurone. It is of a narrowly branching type, with fine, bristle-like twigs terminating the branches (Fig. 4, *c. f.*).

*c. The Fasciculus Communis.*—This remarkable tract was

given the name it now bears by OSBORN ('88) in recognition of the common relationship of several cranial nerves to it. Various authors had noticed the fasciculus communis previous to this time, but they had failed to grasp its significance. STIEDA ('73a, p. 439) had noted the presence of such a bundle in the spinal cord of the selachian; while ROHON ('77, p. 46) described it from the selachian brain under the name *fasciculus longitudinalis lateralis*. The latter writer conjectured that it might pertain to the tegmental system.

In *Mustelus*, the fasciculus communis is a very sharply defined tract extending posteriorly from the VII nerve into the spinal cord, where it lies close beside the gray matter dorso-lateral to the canalis centralis. Its position in the oblongata is shown in Fig. 2, *f. c.* During a part of its course, the visceromotor nucleus is traversed by it. Some of the communis fibres, instead of pursuing a course to the lobus vagi for termination there, turn downward into the fasciculus communis. Thence they are carried posteriorly into the spinal cord for their ultimate distribution.

From the account given by STRONG ('95) of the fasciculus communis in amphibians; and by HERRICK ('99) for the bony fish, I conclude that this tract is developed in *Mustelus* to a conspicuously less degree. The significance of this smaller size for the brain of the selachian is not clear. The communis fibres are essentially viscerosensory, but there have been annexed to the system certain external sense-organs, such as taste-buds and end-buds. There are no observations indicating marked differences between the visceral connections of this system in *Mustelus* as compared with teleosts and amphibians. In fact, the archaic value and deep-seated physiological importance of such connections in all vertebrates would lead us to infer a considerable similarity in related groups. We thus appear to be thrown upon the more recent additions to the system for the explanation. It seems to me that a comparative investigation of end-buds and taste-buds will contribute much toward the solution of questions pertaining to their central tracts.

5. *The Viscero-Motor Nucleus.*

The adoption in this paper of the name *viscero-motor nucleus* expresses the need for a general term which shall include all members of the morphologically continuous column of cells giving origin to the motor fibres of the V, VII, IX, and X nerves. This nucleus is the continuation into the oblongata of the paracentral nucleus of ONUF and COLLINS ('98), and the components having their origin here innervate viscera.

The nucleus is composed of quite large neurones. The only larger ones in the oblongata are the gigantic tract-neurones described in Subsection 3, a. The cells are arranged in a compact cluster, as seen in transverse section, and this is traversed during a part of its course by the fasciculus communis. Fig. 2, *v. m. n.*, illustrates the disposition of the neurones and their characteristic forms.

The cell-body has its form influenced by the number of its dendrites, ranging from triangular to stellate. The dendrites are always several in number. They are massive processes, often arising through such wide bases that it is difficult to say where the line of demarcation between dendrite and cell-body should be drawn. The dendrites branch freely, and the closeness with which the neurones are arranged gives, therefore, a most complicated tangle of interlacing branches.

The internal organization of a viscero-motor neurone is represented in Fig. 47. The nucleus is central, or only slightly eccentric, and it has an evenly rounded contour. The nucleolus is large; there is rarely a subsidiary nucleolus. The nuclear reticulum has a coarse mesh which exhibits great clots or lumps of chromatin at the points of intersection.

The cytoplasm contains tigroid-bodies of various sizes. The largest masses lie in the field of the nucleus. The ones next to the nuclear membrane may assume the form of nuclear caps. At the periphery of the cell, the prevailing form of tigroid is much elongated. It lies parallel with the margin of the cell. Tigroid masses are continued far along the dendrites,

even into the tertiary branches. They are disposed parallel with the course of the dendrites.

In that side of the cell from which the axone arises, the tigroids have a special arrangement. The axone-hillock (Fig. 47, *ax. h.*) is an oval mass of finely granular material, and the tigroid-bodies are packed rather densely round it. The form of tigroid is also less elongated here, merely an irregular lump.

The axone arises directly from the body of the cell. While it is destined to ultimately be a component of either the V, VII, IX, or X nerves, it generally takes quite an indirect course. The usual way is through the medium of the fasciculus longitudinalis dorsalis. An axone passes into this bundle to finally emerge at some other level. In Fig. 47, the axone passes dorsal to the fasciculus communis. There is a bundle of fibres of considerable size lying here, composed chiefly of axones which have emerged from the dorsal longitudinal bundle to enter the nerve-root. Other axones, but these are few in number, may enter the nerve directly. Still others pass into a bundle of arcuate fibres and doubtless enter the nerve on the opposite side. These several paths to the nerves are shown in Fig. 2, *v. m. f.*

The visero-motor neurones have an internal structure which is conspicuously motor in character, the large amount of tigroid substance representing much expenditure of energy here. The large size of the neurone is evidently the correlative of the importance which the system assumes in the innervation of great vital organs. Such innervation requires a nexus with visero-sensory neurones, and the means have already been suggested in the preceding subsection, the interlacing of the axones from the lobus vagi with the dendrites of the visero-motor nucleus. This gives a complete reflex circuit for visceral innervation.

#### 6. *General Cutaneous Nucleus and Spinal V Tract.*

The literature of the portion of the oblongata included here is in some confusion. The older writers did not have methods of investigation which would demonstrate the presence

in this region of several important groups of neurones. They did see that it contains numerous bundles of nerve-fibres, however, some of which run to the cerebellum, and so *pedunculus cerebelli* appeared to be a perfectly satisfactory designation. KINGSBURY ('97) extended the term *Spinal Vth tract* to both the nuclei of the region and the trigeminal fibre-tract proper; such use of a term originally intended to designate a definite group of nerve-fibres is certainly to be avoided as leading to confusion. JOHNSTON ('98b) appears to include a part of this region under his *tuberculum acusticum*. Since there appears to be need for a precise term which shall designate the several nuclei of the general cutaneous system, I therefore propose that the whole be called the *general cutaneous nucleus*.

The general cutaneous nucleus is the continuation into the oblongata of the dorsal cornu of the spinal cord, and it carries its associated tracts with it. Its position will be seen from Fig. 2, *g. c. n.* In structure it is indeed complex, embracing, as it does, three groups of neurones, large numbers of nerve-fibres intercrossing in several directions, the spinal V tract, and many supporting elements. The intrinsic neurones will be considered first.

*a. The Molecular Layer.*—The molecular layer appears in a transverse section as a dorsal cap to the other constituents of the nucleus (Fig. 2, *m. l.*). It is seen to be continuous with the cerebellar crest of the tuberculum acusticum.

The neurones of the molecular layer are of two varieties, the molecular neurones and the neurones of PURKINJE. Both of these varieties are identical with those described in Subsection 7 for the tuberculum acusticum; their morphology will therefore not be given here.

As to distribution, the minute molecular neurones are found scattered through the whole thickness of the molecular layer. The PURKINJE neurones, on the contrary, lie only in the deeper part of the layer, sending their great dendrites into the upper levels. The possible phylogenetic significance of the presence of the molecular layer in this part of the brain will be treated in the theoretical considerations of Subsection 7.

*b. The Substantia Gelatinosa.*—The gelatinous substance of ROLANDO is continued from the spinal cord into the oblongata. It takes on such an intimate relation to the terminating nerve-fibres here that BARKER ('99) has proposed to call it the *nuclei tractus spinalis nervi trigemini*. The Rolandic substance occupies a position high up in the dorsal part of the general cutaneous nucleus, just beneath the cap of the molecular layer, and itself forming an investment for the bundles of fibres and larger neurones of the central mass. The complexity of its structure, and the difficulty of staining it with the usual reagents are facts well known to microscopists. The nerve-cells of ROLANDO's substance in the spinal cord have been studied by VON LENHOSSÉK ('94) from man, the pig, and the mouse; while RAMÓN Y CAJAL ('96) has given us an elaborate description of the oblongata of the mouse. It gives me great pleasure to be able to extend our conceptions of this peculiar formation to the field of the brain of selachians.

In *Mustelus*, the structure of the substantia gelatinosa foreshadows to a remarkable degree the organization which has been described for the higher vertebrates. The neurones are associated in groups; a representative collection is drawn in Fig. 5. The axones and dendrites branch profusely and interlace so closely that the simulacrum of a fine network is given. In this tangle, certain nerve-fibres of the general cutaneous system terminate. Such a fibre is shown in Fig. 5, *g. c. f.*; its arborization may be distinguished from the tangle of neurones in which it lies by the somewhat greater size of its terminal twigs.

The neurones of the substantia gelatinosa, considered morphologically, are of three varieties, all of which are represented in Fig. 5. The one that is present in greatest numbers, giving character to the formation as such, is of quite minute size, and is an extreme example of GOLGI's second type (Fig. 5, *a.*). The cell-body is very small, polygonal in form, and there are a few short dendrites. The axone ramifies immediately into an extremely complex series of branches, constituting the principal member of the tangle mentioned in the preceding paragraph.

These axones are strikingly conspicuous structures when successfully impregnated with chrome-silver.

A second form of neurone is considerably larger in size, its dendrites enter into the tangle referred to, instead of its axone. From a polygonal cell-body, some three or four dendrites radiate indifferently in all directions. The dendrite is of fine calibre, and it branches repeatedly into ever finer twigs. The branching of this system is far less profuse, however, than that of the axone of the first variety described. The difference will be readily seen by reference to Fig. 5, *b*. The axone takes a course out of the gelatinous substance into the deeper parts of the nucleus. It gives off a number of long collaterals during that part of its course lying in the substantia gelatinosa.

The two kinds of neurones just described evidently constitute the physical basis for the central reception of general cutaneous impressions. The first variety, with its short axone, is so concerned entirely, it would seem; while the second one described, having its axone proceeding to deeper regions, is probably involved to an equal degree in both the reception of impressions and in their distribution to deeper levels.

Still a third type of neurone remains to be described (Fig. 5, *c*). From an oval cell-body, a few sparsely branching dendrites arise which lead far out into the surrounding field. The axone takes a course into the deeper nervous matter, giving off only a few collaterals. This form of neurone is found outside the margins of the groups, and apparently is purely associative in function.

*c. The Deeper Neurones.*—The deeper parts of the general cutaneous nucleus are occupied by fibres having courses in several different directions, and by the bundles of the spinal V tract. Neurones are scattered at intervals between the nerve-fibres, with a somewhat more closely crowded area just dorsal to the lobus vagi. Neuroglia is especially abundant in all parts of the nucleus, providing a support for the intricate maze of nervous structures.

The external morphology of a neurone from the middle region of the nucleus is shown in Fig. 6. Such a neurone is

considerably larger in size than any neurone from the substantia gelatinosa. From an elongated-oval or triangular cell-body, three or four dendrites proceed straight outward into the tangle of nerve-fibres and neuroglia. A dendrite is a rather stout process. It has but few branches, and these are of small size. Its surface bears scattering gemmules and minute knobs.

The axone takes its origin directly from the cell-body. It runs in a medio-ventral direction.

Two neurones stained with methylen-blue are represented in Fig. 48. These are from the median collection just dorsal to the lobus vagi. The nucleus of such a neurone is proportionately quite large. It is also eccentric in its position, consequently cells are often found in which the nucleus appears to be in direct contact with the cytoplasmic pellicula at some point. The nucleoli are of some prominence. The chromatic material is also conspicuous. It is distributed in branching strands of some thickness in places, and the several strands may have slight connections.

The cytoplasm is often practically absent at the side of the nucleus. The dendrites are so thick, relatively, at their bases that the greater part of the cytoplasm appears collected in them. The tigroid substance is most abundant in the vicinity of the nucleus. The individual masses here are usually irregular in form and quite small in size. In the basal parts of the dendrites, the tigroid-bodies become elongated. These do not reach far along the dendrites, however.

*d. Termination of General Cutaneous Fibres.*—The nerve-fibres of the general cutaneous system are distributed to the skin of the head without the intervention of specialized nerve-endings. This sensory system has components in the V, IX, and X nerves. There are two principal central stations for these fibres: the general cutaneous nucleus, and the dorsal cornu of the spinal cord through the medium of the spinal V tract. The two termini are really not essentially different, however, since the general cutaneous nucleus and the dorsal cornu are morphologically continuous structures.

Fibres which have their termination directly in the general



cutaneous nucleus may pass into their arborizations in relation to each of several groups of neurones. What is probably the chief mode of termination is shown in Fig. 5, *g. c. f.*, where the fibre is seen entering the tangle of the substantia gelatinosa. At no other point in *Mustelus* is there such a bewildering maze of nervous processes as that presented by the neurones here. So far as structural features may be interpreted, it would seem that the substantia gelatinosa is well adapted for the reception of the most delicate sensory impressions. The large number of arborizations found here indicates the real importance of the group.

Terminations are also to be traced in connection with the deeper neurones of the nucleus. In Fig. 6 there is shown an incoming nerve-fibre, *g. c. f.*, breaking up into its arborization near one of these neurones. The arborization is of the broadly digitate variety, spreading the disturbance over some slight area. The scattered distribution of the neurones at this point is doubtless a correlative of this fact.

Finally, the molecular layer which caps the whole nucleus contains many fibres of quite minute size. This level, with its small branching neurones, and the dendrites from deeper zones, may serve to distribute impressions superficially.

Turning to the spinal V tract, this is a series of bundles of fibres which run posteriorly to the spinal cord. The bundles are scattered through the deeper part of the general cutaneous nucleus; refer to Fig. 48, *sp. V*. General cutaneous fibres may enter the nucleus directly from the nerve of the same side, or through the medium of the arcuate bundles from the opposite side. They may terminate at once in the nucleus, as described above; or they may turn into the spinal V tract for termination farther posteriorly. Some of those present in the tract are doubtless branches of fibres which have terminated in part in the nucleus. The spinal V tract, then, is a means for carrying great numbers of sensory nerve-fibres from cranial nerves to the dorsal cornu of the spinal cord, giving them a second and far wider hold.

The manifold central terminations of the general cutaneous

system must have a significance, if we can but interpret the facts. The system is, primarily, a tactile apparatus for the head. Any one who has watched *Mustelus* exploring with his snout every corner of a new aquarium cannot doubt that tactile impressions from this region must have a large place in the life of the animal. With practically no other check upon his visual sensations than can be derived from poking his nose into things, widely spread central terminations of cutaneous fibres is no more than should be expected.

#### 7. *The Tuberculum Acusticum.*

The tuberculum acusticum is the *trigeminal lobe* of VIAULT ('76), ROHON ('77), and SANDERS ('86); KINGSBURY ('97) has extended the term *cerebellar crest* to the entire structure; while JOHNSTON ('98b) appears to include under his *tuberculum acusticum* all those structures in the oblongata which are homologous with the dorsal cornu of the spinal cord. The term *trigeminal lobe* has been so variously used that it should be dropped from our nomenclature. The earlier writers on the brain of the selachian so designated the tuberculum acusticum, supposing, erroneously so, that the great trigeminal complex, which emerges just beneath its anterior end, must have the origin of its nerve-roots here:

The tuberculum acusticum is the primary terminal station for the acustico-lateral system. Fibres from the lateral line sense-organs and the internal ear are components of the VII, VIII, and X nerves. •

The structure of the tuberculum acusticum embraces a medio-central core in which bundles of nerve-fibres predominate; and an outer investing cap, the cerebellar crest (Fig. 2, *cb. cr.*). The latter, in its outer levels, is morphologically continuous with the molecular layer of the cerebellum, so that the term *molecular layer* is very properly applied here. The neurones of the tuberculum acusticum lie chiefly in the cerebellar crest, with just a few, also, in the central core. Three varieties are to be distinguished: PURKINJE neurones, granular neurones, and molecular neurones. I have so designated them because

each is the equivalent in every way of the element bearing such a name from the cerebellum.

*a. Molecular and Granular Neurones.*—The molecular and the granular neurones do not call for any extended description here, since they are directly comparable with the cerebellar representatives described at length in Section V.

The molecular neurones are the most numerous of the three varieties peculiar to the tuberculum acusticum. They are found scattered throughout the molecular layer, most abundantly in the deeper levels. Each has the characteristically small cell-body with slender dendrites radiating from it.

The granular neurones are far less numerous. They lie just within the base of the molecular layer, but there are not enough of them to form a distinct zone. Stained with methylen-blue, they exhibit the typical dense nuclear structure and the small amount of cytoplasm.

*b. Purkinje Neurones.*—The phylogenetic interest attaching to the presence in the oblongata of these elements calls for more special notice. The PURKINJE neurones of the tuberculum acusticum are not disposed in any regular order. They lie scattered between the deeper molecular neurones, and they are also found among the granular neurones. Their dendrites are always directed toward the limitans externa, whatever the situation of the cell-body may be, although the exact course may be at a considerable angle to the perpendicular. The axone always passes inward. Refer to Fig. 2, *t. a.*

The cell-body is slightly oval or even perfectly circular in outline (Fig. 7). The particular form assumed appears to be correlated with the position of the dendrites. The gnarled character of a dendrite is quite evident. There are three or four of them, terminating in blunt tips. A dendrite bears few branches, or none at all, and its surface is studded with numerous thorny gemmules of various sizes, some of them quite large.

The axone arises from the internal border of the cell. It takes a ventral course through the intervening nervous tissue into a bundle of arcuate fibres. Its ultimate distribution has not been definitely followed.

The internal structure presents a large nucleus with deeply staining chromatin in the form of a reticulum; and cytoplasm somewhat less in quantity than in the cerebellar neurone, and holding less tigroid substance.

From the above description of the morphology of the neurone of PURKINJE from the tuberculum acusticum, it will be evident that it is strikingly like its earlier-known representative in the cerebellum. Compare, also, Fig. 7 with Fig. 13. The neurone from the tuberculum acusticum (Fig. 7) is merely slightly smaller in size, with a dendritic top which branches somewhat less. The presence of conspicuous gemmules is characteristic of both. We shall take occasion to point out further on that the cerebellar neurone is to be regarded as the more fully developed derivative of this element from the oblongata.

*c. Termination of Acustico-Lateral Fibres.*—The fibres of the acustico-lateral system enter the tuberculum acusticum through the medium of the thin neck joining the acusticum with the general cutaneous nucleus below. This fact is expressed in Fig. 2, *a. l. f.* It appears, so far as they are traceable, that these fibres have passed over from the opposite side in the arcuate bundles. Penetrating the core of the acusticum, the fibres are at first associated in groups, but these soon become dissolved and the individual members spread through the outer levels. The fine terminal branches pass through the thorny dendritic tops of the neurones of PURKINJE, and the final arborizations are to be frequently observed near the bodies of the PURKINJE cells. Such a termination is shown in Fig. 7, *a. l. f.* The nerve-fibre divides at some distance from the cell into several twigs, and from the portions of those nearest the cell-body several small terminal twigs arise which form an arborization quite near to the cell. There is given in this way a direct nexus between the acustico-lateral fibres and the most conspicuous neurone of the tuberculum acusticum. Other fibres of minute size evidently terminate in the molecular layer between the small molecular neurones. Even here there would be an indirect connection with the PURKINJE neurones, for these send their dendrites into the molecular layer.

Fibres are also to be seen in numbers which do not terminate in the tuberculum acusticum at all. Some of these remain in the central core, continuing anteriorly; while others are branches of fibres which have taken a course into the acusticum for partial termination there. All of these pass upward to the cerebellum; they will be duly considered in Section V.

*d. Theoretical Conclusions.*—It has already been pointed out that acustico-lateral components are not present as such in spinal nerves. Waiving the question of the origin of the system as a whole, it will not be out of place to consider here certain problems relative to its primary centre, the tuberculum acusticum.

The position which the tuberculum acusticum occupies in the oblongata is indeed significant, superposed, as it is, on the cranial representative of the dorsal cornu, the general cutaneous nucleus. This fact can only be taken to mean that the tuberculum acusticum is phylogenetically the younger of the two structures in question. In Subsection 6 it was shown that the general cutaneous nucleus has the archaic structural features of the dorsal cornu capped with a molecular layer continuous with the cerebellar crest of the acusticum; and that there are present here both the molecular cells and the neurones of PURKINJE. Now this structural continuity may signify that the acusticum has been derived from the general cutaneous nucleus in the phylogeny of the vertebrate nervous system. Of course it will be necessary to have a thorough study of the embryology of this region in the lower vertebrates before such a conclusion can receive unqualified support. Then, too, the rise of the tuberculum acusticum has been but one feature in the evolution of the lateral line system as a whole, and so we may confidently expect some assistance from the further study of the affinities of its sense-organs.

There is somewhat more solid ground for the belief that the tuberculum acusticum has itself given origin to a very important region of the brain, the cerebellum. The full evidence on this point will be presented in Section V, Subsection 6.

8. *Supporting Elements.*

*a. Ependyma.*—The ependyma of the oblongata constitutes the membrana limitans interna throughout, of course, but the degree of differentiation covers a wide range. The simplest condition is found in the tela choroidea, for the cells here do not give origin to ependymal fibres. This might be called the epithelial phase of development.

The first step in the differentiation of ependyma occurs in the dorso-lateral region of the oblongata, embracing the tuberculum acusticum and the adjacent part of the general cutaneous nucleus. The ependymal cells are rather narrow here, giving a larger number per surface area. From the tip of each cell, a very slender ependymal fibre pushes its way through the nervous matter to the limitans externa. The fibre does not branch, and its general course is a straight one, although the details of its path are very irregular indeed, sharp turns of small size occurring along its whole length. While the diameter of the fibre as a whole is quite slender, its size is increased at irregular intervals by beads and small knobs. Consult Fig. 8.

A slightly more advanced condition is to be noted for the ependyma of the ventral region. The ependymal cells in the floor of the fourth ventricle are larger than those described above, and their fibres are also much stouter. The general course of these fibres is shown in Fig. 2, *ep.*; and the details of two fibres are given in Fig. 9. It is to be noted that the fibre extends entirely to the limitans externa, that it bears no branches, that its course is free from sharp turns, and that its diameter is varied by nodes and thickenings of various shapes and sizes. Groups of these fibres form radiating bands through the formatio reticularis, and their evident purpose is to provide stays for the vast number of longitudinal and arcuate nerve-fibres which characterize this part of the oblongata.

The ependyma attains its highest differentiation in the lobus vagi; see Fig. 10. The fibres do not reach the surface, and they give origin to a most complicated series of branches at the level occupied by the neurones of the lobus. The prox-

imal part of the fibre is quite stout and somewhat irregular in its course. The distal part becomes dissolved in branches, the terminal twigs of which are minute. The interlacing branches form a support for the neurones and nerve-fibres proper to this region.

*b. Neuroglia.*—The neuroglia of the oblongata is, like the ependyma, present in great diversity of form, but the various elements are referable to two general classes. One, the well-known astrocyte, is distributed in every part of the oblongata where there are nerve-fibres in numbers—in the roots of nerves, in special tracts, in centres where many fibres have their termination, and in the formatio reticularis. The special form of the astrocyte depends, to some extent at least, upon the density with which the nerve-fibres are arranged. At points where there has been little pressure, the rounded form of the cell-body may be retained (Fig. 3, *ng.*). In certain closely packed tracts, the cell is squeezed into lenticular form. In centres where many minute fibres interlace, there may be hardly any body to the cell at all, the matter being chiefly in the radiating processes (Fig. 11). In every instance, the processes exhibit tortuous irregularities due to their insinuation between the nerve-fibres among which they lie.

Another type of neuroglial cell appears to be characteristic of the ventral part of the oblongata, occurring in some numbers in the formatio reticularis (Fig. 3). The cell-body is large, elongated, with great processes emerging from its ends and a few smaller ones from its sides. The large processes take a course in the radius of the oblongata. They give origin to secondary and tertiary branches, the finer ones of which lie at right angles to the course of the principal branch. The whole system does not spread widely, but has the appearance of compression in one plane.

The astrocyte is evidently an important supporting element for the individual nerve-fibres between which its processes twine. The second class of neuroglial cell described seems to be adapted to the supporting of bundles of nerve-fibres. The arcuate fibres of the formatio reticularis pass in groups through

the spreading brush of such neuroglial processes and are thereby given support.

9. *Summary of the Oblongata.*

The structural features of the oblongata of *Mustelus* may be homologized with those of the spinal cord to an unusual degree of clearness.

The ventral cornu is represented by the nucleus of the VI nerve, and by the scattered commissural and tract-neurones of the formatio reticularis.

The lobus vagi is, morphologically, the centre of the viscerosensory system, but there has been annexed to it a complex of peripheral sense-organs. It has come to be, therefore, the centre for the entire communis system, components of the VII, IX, and X nerves. Endings are found related to neurones of the Golgi II type. These send their axones toward the visceromotor nucleus. Fewer fibres of the system enter the fasciculus communis than in either the teleosts or the amphibians.

The visceromotor nucleus is the representative of the paracentral nucleus. It is a morphologically continuous column of cells giving origin to the motor fibres of the V, VII, IX, and X nerves innervating viscera. The axones do not enter their nerve-roots directly, as a rule, but through the medium of the fasciculus longitudinalis dorsalis. Some appear to cross to the opposite side. Dendrites from the nucleus come into relation with axones of the lobus vagi.

The general cutaneous nucleus is the homologue of the dorsal cornu. It is the primary centre for the general cutaneous components of the V, IX, and X nerves. The substantia gelatinosa contains groups of small Golgi II neurones forming dense, felt-like tangles; many terminal arborizations are found in these. Other terminations occur near larger neurones lying in the deeper parts of the nucleus. Many fibres of the system do not terminate in the nucleus, but are carried posteriorly as the spinal V tract for ultimate termination in the spinal cord.

The tuberculum acusticum is a phylogenetically young



structure, not derivable from the cord directly. It is the primary centre for the acustico-lateral system, components of the VII, VIII, and X nerves. There are present, neurones of the molecular, granular, and PURKINJE types, identical with those of the cerebellum. Terminations occur in the molecular layer, and near the neurones of PURKINJE. The PURKINJE neurones send their axones ventrally in the arcuate bundles. The cerebellar crest is morphologically continuous with the cerebellum. There is ground for believing that further investigation will derive the acusticum from dorsal cornu structures.

Supporting elements are present in the oblongata in great numbers. There is traceable a wide range of developmental forms of both neuroglia and ependyma.

#### SECTION V. THE CEREBELLUM.

The cerebellum of *Mustelus* is of large size in comparison with the adjacent brain-segments. In the adult animal, it is of sufficient longitudinal extension to overhang the larger part of the midbrain in front, and also much of the oblongata behind (Fig. 1, *cb.*). The base is only a third as great, however, indicating the smaller prototype from which the organ has been evolved. In fact, this cerebellum occupies an intermediate position in the phylogenetic scale, standing midway between the simple plate-like cerebellum of the cyclostome, the dipnoan, or amphibian, and the solid mass with radiating laminae characteristic of the mammal. It is essentially a great bulbous dilatation of the dorsal side of the neural tube, the wall of which has been thrown into folds as the process of growth thrust the vesicle against the unyielding and more slowly expanding cranium. So, instead of a solid central mass of nerve-fibres covered with layers of gray matter, we find in *Mustelus* a hollow organ, the fourth ventricle extending freely into it and ramifying through its several folds. The folds, therefore, are simply doublings in the cerebellar wall, and are fundamentally different from the solid laminae familiar to us in higher vertebrates.

The arrangement of the structural elements of the cere-

bellum is readily followed, for in no other part of the brain are distinctions more clearly marked. Superficially, there is the molecular layer (Fig. 12, *m. l.*); the granular layer lies next to the ventricle, or is separated from it only by the basal fibres (Fig. 12, *g. l.*); between the two, there is the layer of PURKINJE (Fig. 12, *p. l.*).

The nerve-fibres of the organ are found in two well-defined groups, the basal fibres and the median fibres. The basal fibres (Fig. 12, *b. f.*) enter the posterior region from the oblongata and soon become dissolved in the outer layers. These fibres lie next to the ventricle, and they supplant the granular layer entirely during their course, or at least displace it quite largely. The median fibres are disposed in scattered bundles which lie in the outer part of the granular layer just beneath the cells of PURKINJE. The bundles take two general directions: transverse, (cut across in Fig. 12, *m. f'.*); and longitudinal, extending parallel with the structural zones (Fig. 12, *m. f.*).

#### 1. *The Neurones of Purkinje.*

The neurones of PURKINJE are the largest, and by far the most impressive structural elements of the cerebellum. Their cell-bodies are disposed in a thin stratum intercalated between the molecular and the granular layers. At those points where the granular layer is absent, the PURKINJE cells come into direct contact with the layer of basal nerve-fibres, instead. As to superficial distribution, the neurones follow a well-defined rule (Fig. 12, *p. l.*). They are most numerous on the side of a cerebellar fold, often several cells in depth here, and not infrequently having their cell-bodies in contact. At the summit of the fold, there are wider spaces between the individual cells; and for a small space at the bottom of a fold, the cells are absent altogether. The posterior fold of the cerebellum has a part of its area without PURKINJE neurones.

Fig. 13 illustrates the features of external morphology characteristic of a neurone of PURKINJE. The cell-body is situated, as already noted, at the base of the molecular layer. The dendrites, therefore, grow upward into the molecular layer, and

to their presence here is due, in part, the marked striation perpendicular to the surface which is so characteristic of the superficial zone.

The axone always arises from the base of the cell-body, and it pursues a horizontal course for some distance. It then turns downward through the granular layer to enter the system of fibres leaving the cerebellum. Where the granular layer is absent, the axone may be traced into the layer of basal fibres for a still greater horizontal course. The axone is remarkable for the fact that it does not give off collateral branches.

The cell-body appears to have its form determined quite largely by the number and disposition of the dendrites arising from it. It may be rounded, oval, or even triangular in outline. The longer axis of the cell, while usually perpendicular to the surface of the fold, may be oblique or still farther tilted over from the orientation characteristic of it for the higher vertebrates. Even the size of the cell is influenced by its position. The diameter is greatest in those cells lying at the part of the fold where the side curves abruptly into the summit. On the sides of the fold, the size is remarkably less, and the dendrites pass outward at a wider angle, often causing the cells here to assume a horizontally elongated form. The cell studied by SZCZAWINSKA ('98) evidently was of this latter type.

The internal structure of the PURKINJE cell is demonstrated less readily with methylen-blue than is the case for most nerve-cells of *Mustelus*. In successful preparations, however, the cytoplasm is found to hold tigroid masses of triangular or spindle-shaped form. These bodies are neither large in size nor many in number. There are always several of the greatest diameter arranged near to and concentric with the nuclear membrane. The thick bases of the dendrites have small, narrow, lenticular tigroids distributed sparingly as far as the level of the first great branches. The character and distribution of the tigroid-bodies will be seen by reference to Fig. 49.

The nucleus of the cell lies in a basal position, but it is always bordered by some little thickness of cytoplasm. The form is oval or circular, with an almost even contour. There is

one large nucleolus, with a subsidiary nucleolus in some cells. The nuclear reticulum has a rather fine mesh; large granules of chromatin occur at the points of intersection.

The dendrites arise from the peripheral side of the cell-body, and they pass at once into the molecular layer, taking a direct course for the *limitans externa*. The size of a dendrite is maintained without marked diminution, the tip, in fact, being so large and blunt as to give a club-like appearance to the whole process. The mode of branching is far simpler than that of the corresponding mammalian neurone. While the dendrite of the latter ramifies to an extraordinary degree, it is rare to find branching carried beyond the tertiary divisions in *Mustelus*; compare my Fig. 13 with Plates 14 and 15 of STARR's Atlas ('96). From its greater simplicity, the selachian neurone of PURKINJE corresponds, in a broad way, to the embryonic condition of the higher form. The branches are spread in one plane, like a plant trained on a wall, and this plane lies transversely to the cerebellar folds. The course of the branches in this plane is less wide than for mammals, causing the whole top to present a markedly more compact appearance. The surface of a dendrite has the conspicuous roughness characteristic of this neurone wherever found. The gemmules, to which this roughened surface is due, are of several different sizes, ranging from mere points through slender spines and stouter thorns to knobs and mushroom-like excrescences which rise far above the general level. The extent of receptive surface of the entire dendritic series is thus increased to a very considerable degree.

The part which the neurone of PURKINJE takes in the economy of *Mustelus* will be discussed in Subsection 5.

## 2. *The Molecular Layer.*

This is the external layer of the cerebellum (Fig. 12, *m. l.*). It conforms throughout to the contour of the several folds into which the cerebellar wall is thrown. Its thickness is carried with considerable uniformity, but in most of the regions the depth of matter is only about half as much as that of the granular layer within.

The molecular layer is characterized by the predominance of fibrous elements and the fewness of nerve-cells. In contrast with the mass of densely-packed, conspicuous cells of the granular layer, the outer region presented hardly more than a minutely punctate appearance to the earlier investigators who had recourse to nothing more differential than the general stains in use at that time. Hence *molecular* seemed an appropriate descriptive term for this layer.

Through the use of modern methods, we find the molecular layer to have a few proper neurones of small size, but the great mass of substance consists of fibrous material, between the parts of which the nerve-cells are intercalated. But, it is certainly a fact worthy of mention, the fibrous constituents of the layer do not have their origin there, penetrating it, rather, from deeper levels. The dendrites of the PURKINJE neurones, and the processes from the neuroglial cells comprise one great class of constituents. These take a course perpendicular to the surface and cause the vertical striation which is so marked a feature of the region. Then, too, the neurones of the granular layer send their axones outward into the molecular layer for a T-shaped division, each thus giving origin to a pair of fibres. These branches take a course across the sagittal plane of the cerebellum, parallel at once with the limitans externa and the lateral surface of a fold. To the presence of these fibres, cut across in such numbers in a sagittal section of the cerebellum, the characteristically punctate appearance of the molecular layer is chiefly due. Finally, it should also be noted, there are numerous terminations in the molecular layer of nerve-fibres which have entered the cerebellum from some other region of the nervous system. Such terminating fibres branch so as to distribute the endings over a considerable superficial area.

It will thus be seen that the molecular layer is really a tangle of nervous tissue, a series of paths where many associations may be formed. This topic will be discussed more at length in the fifth subsection.

The neurones proper to the molecular layer are, as already noted, but few in number, and those present are scattered be-

tween the nerve-fibres. The external morphology of one of these neurones is represented in Fig. 14. From a small, almost perfectly spherical cell-body, three or four dendrites radiate, branching in what is an approach to a dichotomous manner. The dendrites are not thick at their bases and they become lost to view before proceeding far, owing to the fineness of the terminal twigs. The surface of a dendrite is almost perfectly smooth, there being only the faintest indication of gemmules, but there are small varicosities at irregular intervals which produce slight variations in the thickness.

The internal organization of the cell presents a large, rounded nucleus which is enveloped by a stratum of cytoplasm of no great thickness (Fig. 50). The cytoplasm contains tigroid substance distributed in granules of the most minute size, mere points even when highly magnified. The chromatin is distributed along a linin reticulum of such fine mesh that the nucleus is thereby often made to appear almost perfectly black. There is a single nucleolus.

In mammalian neurology, the molecular layer is known to have two varieties of cells: (1) stellate cells, the processes of which lie freely in the layer; and (2) basket cells, somewhat larger in size, occupying the deeper levels of the layer, and having their axones associated with each other in such a way as to form plexuses or baskets around the cell-bodies of the PURKINJE neurones. The latter type of cell is, of course, the more specialized of the two. It is therefore interesting to note that it is not represented in *Mustelus*, but that all of the molecular cells correspond, rather, to the stellate cells of higher vertebrates. Such a result is, however, to be expected in a brain of lower phylogenetic value.

### 3. *The Granular Layer.*

The granular layer lies internal to both the molecular layer and the neurones of PURKINJE. It is somewhat irregular in its distribution. At many places it is twice as thick as the molecular layer, notably at the summits of the great folds; while it tends to decrease in extent as the bottom of a fold is reached.

A sagittal section of the entire cerebellum shows a few regions where the granular layer is absent altogether (Fig. 12, *g. l.*).

With nuclear stains, the granular layer appears to consist of a vast number of densely packed, rounded nuclei, from which fact the names *granular* and *nuclear* have been applied as descriptive terms. It is only through the application of metallic impregnation that the real character of the elements and the relations between them have been determined. When thus demonstrated, there are to be recognized neurones of two distinct varieties, the granular, proper, and the GOLGI neurones.

*a. The Granular Neurones Proper.*—Nearly all of the neurones comprising the granular layer are included in this class. The distinctive features of such a neurone (Fig. 15) embrace a rounded cell-body having a few short dendrites, and an axone which ascends through the levels of the granular layer above its point of origin to the molecular layer, where it divides in a T-like manner.

The size of the cell-body varies slightly, but it is always smaller than a neurone of PURKINJE. As to shape, there is considerable diversity. The derivative form appears to be a rounded one, but this has been subjected to much modification by the origin of the dendrites so that triangular, rectangular, and various polygonal outlines are given.

The internal structure of the cell, (Fig. 51), consists chiefly of the nucleus, only the faintest halo of cytoplasm being visible at any point; even the bases of the dendrites can hardly be recognized with purely cytological stains. Demonstrated with either methylen-blue or iron haematoxylin, the nucleus is found to contain a few very coarse and irregular chromatin granules strung on fine interlacing threads of linin. The presence of a nucleolus is doubtful, at least it is difficult to distinguish one from the masses of chromatin. Fig. 51 also shows how closely these neurones are packed.

The dendrites are three or four, only, in number, arising from the cell-body at approximately equidistant points (Fig. 15). A dendrite is short and nearly always relatively stout. Its course involves sinuous curves. It branches but rarely until

the tip is reached, where it dissolves into a brush or a series of hooks spreading over a relatively considerable area. There are no gemmules.

The axone is exceedingly slender. It may arise directly from the cell-body, but it usually takes its origin from one of the dendrites, either near the base or at some distance from the cell; Fig. 15 illustrates the two modes of formation. The course of the axone is invariably peripheral, pushing through the intervening thickness of the granular layer into the molecular layer. At the boundary between the two layers, the course changes abruptly to a horizontal one for a short distance, and hence the entire course of an axone can rarely be traced in one section. In the molecular layer, the axone divides into two branches which, with the original stem, form a T-shaped figure (Fig. 16). The two branches pursue a course parallel with the surface of the cerebellum and the sides of the fold in which they run. It is thus seen that they pass through the dendritic tops of the neurones of PURKINJE, comparable to telephone wires passing through the tops of the trees along a highway.

*b. Golgi Neurones.*—A few neurones of the granular layer have an altogether different character from the ones just described. These lie in the upper levels of the layer. Such a neurone is shown in Fig. 17. The cell-body is always a little larger than that of the typical granule neurone, and its form is more rounded. A few club-like dendrites radiate from it for a short distance, branching but sparsely. The size of a dendrite is increased at intervals by slight swellings.

The axone passes downward into the deeper levels of the granular layer, instead of upward. It gives off collateral branches soon after its origin, and it breaks up into a number of fine terminal twigs before any great distance has been traversed.

This neurone is homologous with the variety described by GOLGI ('94) from the human cerebellum, and by him made a representative of his *second type* of nerve-cell. The branching of the axone is far less profuse, however, than in the mammal.

We thus see that the granular layer of the cerebellum of *Mustelus* is marked by the presence of the same varieties of



neurones which characterize this layer in higher vertebrates. The morphology is somewhat more simple in the selachian, as should be expected, but it is a suggestive fact that the structural plan of higher forms is here outlined in its essential features.

#### 4. *Supporting Elements.*

The supporting elements of the cerebellum are referable to both the ependymal and the neuroglial series, the former being limited to the granular layer, and the latter to the molecular layer. The structure in each instance appears to be particularly adapted to the supporting of the nervous mechanisms peculiar to these regions.

*a. The Ependyma.*—The ependyma of the cerebellum presents the usual palisade of closely crowded cells forming the *membrana limitans interna* (Fig. 18). The cell-body is irregularly pyramidal in form, the sides rarely tapering evenly to the apex but exhibiting more or less bold curvatures of outline.

From the apex of the cell-body, a process, the ependymal fibre, arises, and this pursues a course through the structures of the granular layer to near the outer limit of that zone. I have not found a single instance where one of these fibres passed beyond the granular into the molecular layer, a fact of some possible phylogenetic value, indicating the more ancient character of the internal region.

The ependyma-fibre is relatively stout, but its diameter is far from uniform. There are fibres which have portions of the length four or five times the thickness of the intervening parts; see Fig. 18, *b*. Occasionally, knobs and other rounded thickenings are found, particularly at angles where the course of the fibre changes abruptly. The trend of the fibre is never conspicuously irregular, only such slight turns and windings occurring as might be expected where obstructions are present during the period of growth. The general trend is directly toward the surface of the cerebellar fold, the several fibres lying more or less nearly parallel with each other.

The degree of branching exhibits wide diversity. Certain

fibres (Fig. 18, *a*) have some half-dozen principal branches of various lengths, none of them very long nor diverging widely from the main stem; besides the principal branches, there are shorter twigs distributed sparingly along both the main stem and its ramifications. Other fibres (Fig. 18, *c*) are so beset with a multitude of small twigs, quite irregular in their branching, that the whole series is given much the appearance of a long and cylindrical brush. Between these two extremes, there are every intermediate condition of branching forms.

The ependymal fibres lie quite near to each other, and the many processes from them constitute an interlacing tangle, the profusion and extreme delicacy of which cannot be adequately represented in any drawing. In order to appreciate the significance of this dense supporting framework, the vast number of the granular neurones must be recalled. Here we find the means by which these nervous elements are given that support which is one of the primary conditions for their activity.

*b. Neuroglia.*—The neuroglia provides a support for the outer structures of a cerebellar fold, just as the ependyma functions within. The characteristics of neuroglial elements are shown in Fig. 19, *ast.* and *bg. f.* The cell-body lies at the junction of the molecular and granular layers, between the cells of PURKINJE. Two conditions are to be distinguished. One variety (Fig. 19, *ast.*) has a cell-body of quite irregular outline from which many processes radiate. These processes rarely branch. Some of them may proceed to a distance equal to several times the greater axis of the cell, but most of the branches are far shorter. They are placed so closely along the margin of the cell that the whole has something the effect of a halo. These cells are clearly homologous with the astrocytes of higher vertebrates.

The other type of neuroglia-cell (Fig. 19, *bg. f.*) is referable to the category of BERGMANN'S fibres of the mammalian cerebellum. The cell-body has fewer processes than the astrocyte, but it gives origin to one stout fibre which takes a peripheral course, without branching, through the entire thickness of the molecular layer. The path of the fibre is not one directly

toward the surface, for it runs almost parallel with the layer of PURKINJE neurones for a short distance; it then turns upward, terminating at the limitans externa in a conical expansion. During the proximal part of its length, it bears fine processes similar to those emerging from the cell-body. The distal part of the fibre has a remarkably vast number of fine processes. These may remain separate from each other, but at intervals they become matted together so closely that the whole has the appearance of felt or even that of a solid.

The account given by SCHAPER ('98) of what he took to be BERGMANN's fibres does not correspond with my findings in several particulars. This author does not mention the processes of the cell-body, nor do his figures show them. It may be that his preparations were insufficiently impregnated. Weight is given to such a possibility from the fact that he did not find astrocytes at all. It is certainly of some phylogenetic interest that BERGMANN's fibres appear to be derived from astrocytes. I have found numerous instances where transitional forms are recognizable, linking the extremes of the simple astrocyte with the one provided with a long process, the fibre of BERGMANN.

The position occupied by the cell-body of a BERGMANN's fibre is also significant. KÖLLIKER ('96, p. 368) states that at birth BERGMANN's fibres in mammals lie at the boundary of the granular and molecular layers, and that during growth they normally migrate into the granular layer. Now the permanent position of BERGMANN's fibre in *Mustelus* corresponds to the embryonic state in the mammal. An additional comparison may be instituted regarding the form of the fibre, the adult element of *Mustelus* remaining simple, while the mammalian fibre becomes much branched. That the condition in *Mustelus* corresponds to the embryonic stage of development in higher vertebrates is, of course, no more than should be expected.

The physiological interpretation of the cerebellar neuroglia is not difficult. The numerous processes from both the astrocytes and BERGMANN's cells provide a delicate suspensory apparatus for the neurones of PURKINJE. The great BERGMANN's fibres, reaching upward as they do through the molecular layer,

may be likened to so many telegraph poles; and the matted tangles extending laterally from these are the cross-bars for the wires. The wires to be supported, following out our comparison, are the horizontal axones of the granular neurones, which, as we have already noted, extend through the molecular layer in large numbers.

#### 5. *Architecture and Physiology of the Cerebellum.*

It is now a well established fact that the principal function of the cerebellum is to preside over the equilibration of the body. Moreover, a fairly direct connection is traceable between the morphology of this segment of the brain and the nature of the muscular activities which are characteristic of the animal. To the student of comparative neurology, therefore, the cerebellum holds problems of a special order, and is ever potential with no mean interest.

We have seen that the cerebellum of *Mustelus* retains an external form of a far lower order than that found in the bird or mammal. The internal organization is not so inferior, however, as we might, from this fact, be led to infer. The architectural features of the lower and the higher types are so similar that the contrast is really one of degree and not one of kind. In both instances, the same sorts of neurones are present, grouped in a similar way, and related to each other physiologically in essentially the same connections. This remarkable identity of features can only be interpreted to mean that the cerebellum became established in its organization quite early in the history of vertebrates.

Undoubtedly, the key to the significance of cerebellar structure and physiology is to be looked for in the neurones of PURKINJE. These striking cells, with their characteristic tree-like tops, apparently have all of the other structural elements present arranged contributory to them. Imbedded in the midst of the nervous matter, supported by the interlacing processes of the neuroglia there, a PURKINJE neurone sends its great branching dendrites outward into a veritable maze of possible physiological connections, for such the molecular layer really

proves to be. We have seen that the granular neurones contribute their axones to a series of fibres passing horizontally through a row of spreading PURKINJE dendrites; that the neurones of the molecular layer are themselves radiately connecting paths; and, finally, that the incoming nerve-fibres, those arising outside the cerebellum, end, some in the granular layer, others taking a longer course into the molecular layer. These several elements evidently have no other purpose than the bringing of all incoming impressions, through one path or another, to bear upon the neurones of PURKINJE. The great spreading top of a PURKINJE cell is obviously a device for providing a large receptive surface for such impressions, while the many thorn-like gemmules with which the dendrites are studded serve as a yet greater extension of that surface, or, perhaps, make one which is more readily impressed. The axone of the cell takes a more or less direct course out of the cerebellum, carrying the resultant of the nervous interactions to the proper point for ultimate distribution. If it is the purpose of the whole series of cerebellar elements to provide a central mechanism of equilibration, then the neurone of PURKINJE is certainly the centre of that mechanism. The various nerve-fibres sweeping into the cerebellum may terminate in several ways and at diverse levels of the organ, but everywhere there are devices for connecting them physiologically with the neurones of PURKINJE, which receive all and preside over all.

The researches of LEE ('92, '93, '94, '98) upon equilibration in fishes have shown with what nice discrimination these aquatic animals balance themselves, devoid, as they are, of many sources of impressions possessed by terrestrial vertebrates. Doubtless a large number of equilibril impressions are derived from the visual mechanism of the fish. Axones from the roof-nucleus of the midbrain pass backward into the cerebellum; and it will be shown in Subsection VI that there is a most intimate association between the roof-nucleus and optic terminations. Another source of equilibril impressions is to be found in the fins and body musculature, entering the cerebellum through the tractus cerebello-spinalis. But the work of LEE

clearly demonstrates the overshadowing importance of the piscine ear as a peripheral organ of equilibration. In fact, his latest research ('98) makes it clear that the great ear of *Mustelus* is not a true auditory organ at all, but that its several parts are to be interpreted from the standpoint of the equilibrium sense. The large nerve-tracts from the ear to the cerebellum are, therefore, definitely significant, being the connecting fibres between the central mechanism and its most important peripheral organ. It also appears that not only does the ontogeny of the ear show its relationship to the lateral line organs, but the functions in the two instances are comparable as well.

An analysis of the habits of *Mustelus* will, it appears to me, go far toward explaining the disproportionately great development of both the ear and the cerebellum which we find the animal to have. This shark, although a comparatively small representative of the group, is, withal, a restless hunter of the seas, ever urged onward by an appetite which, apparently, has no bounds. Continually suspended in a fluid medium, and compelled to balance itself at every turn, the animal requires a precise mechanism of equilibration. This is to be found, in the main, in both an ear and a cerebellum developed to a degree out of all proportion to the scale occupied by the creature as a whole.

#### 6. *Evolution of the Cerebellum.*

Evidence of the origin of one brain-structure from another is usually of the most meagre value, but it appears as though it were now possible to weave together a few scattered threads in the evolution of the cerebellum. SCHAPER ('94) has called attention to certain facts in the embryology of the teleostean cerebellum which may be taken as the starting point. The cerebellum arises in ontogeny, not as a brain-segment having the full value of the others, but as a paired thickening in the parietal wall of the neural tube at the anterior end of the oblongata. These thickenings grow upward and meet each other in the median line. SCHAPER has since extended his studies to all classes of vertebrates, and he finds ('99) that the anterior

limit of the bilaterally symmetrical anlage may be definitely fixed, coinciding with the boundary between the primary mid- and hindbrain vesicles. The posterior limit of the future cerebellum is by no means clear, however, for it seems to merge backward into the oblongata. These are certainly significant facts.

It was shown in Section IV, Subsection 7, that the molecular layer of the cerebellum is continuous with the cerebellar crest of the tuberculum acusticum, maintaining essentially the same morphological characters throughout. It was also shown that there are present in the tuberculum acusticum neurones which are identical with those of the cerebellum—molecular neurones, granular neurones, and PURKINJE neurones; the last two varieties are not grouped into definite strata, however. The presence of granular neurones in the acusticum is worthy of remark, but the greatest weight must be attached to the finding of PURKINJE neurones here. These neurones were long supposed to characterize the cerebellum alone, and their strikingly peculiar appearance makes them readily identified. The neurones of PURKINJE from the acusticum of *Mustelus* agree with those from the cerebellum as to size, general form, shape and character of dendritic top, and even in the presence of the spiny gemmules so characteristic of this nervous element. There can be no question as to their morphological identity in *Mustelus*. JOHNSTON ('98b) has found PURKINJE neurones in the acusticum of *Acipenser*, somewhat smaller and simpler than those of the cerebellum, but undoubtedly equivalent. Similar results will probably be obtained in all of the simpler vertebrates.

It may be concluded, in the light of these embryological and structural facts, that the cerebellum has arisen in the phylogeny of vertebrates as a fused outgrowth of the pair of tubercula acustica. The acusticum is the primary end-station, as we have seen, for the nerves of the ear and the lateral line organs. The cerebellum has been differentiated from the primary ending as a special centre for presiding over equilibration. Parallel with the increasing development of the equilibrial sense in ver-

tebrates, the cerebellum has gradually acquired associations with other than the original source, so that the fibres entering the organ have ever been growing more numerous, and the bulk of the fibrous centre consequently more massive.

#### 7. *Summary of the Cerebellum.*

The cerebellum of *Mustelus* is of relatively large size, and, although remaining in the primitively hollow condition, its wall has the same essential plan of structure as the organ in higher vertebrates.

Neurones of PURKINJE form a zone, crowded at certain points, between the molecular and granular layers. Such a neurone has the structural features characteristic of its mammalian representative, but with a simpler branching of dendrites. Its office is to receive incoming equilibratory impressions.

The neurones of the molecular layer are few in number. They are all of one variety.

The neurones of the granular layer are of two kinds: GOLGI neurones and granular neurones. The former lie in the upper strata of the layer. The granular neurones are strikingly like those of higher vertebrates; their axis-cylinders branch in a T-shaped manner in the molecular layer, mediating between many incoming fibres and the dendrites of the neurones of PURKINJE.

Ependyma is developed into a profusely branching fibre which extends through the granular layer, only.

Neuroglia provides a supporting framework for the neurones of PURKINJE and the molecular layer. Both astrocytes and BERGMANN'S fibres may be recognized, but there are transitional forms indicating that the latter have been derived from the former.

The large size of both the ear and the cerebellum of *Mustelus* is to be explained by the swimming habits of the animal. The structures have an equilibratory value.

The cerebellum has apparently arisen in the phylogeny of vertebrates as a fused outgrowth of the pair of tubercula acustica, a specialization of that part of the oblongata forming the original terminal station for the acustico-lateral system.



## SECTION VI. THE MIDBRAIN.

The midbrain of *Mustelus* has retained to a marked degree the features characteristic of this cerebral vesicle in its primitive condition. Its ventricle has been so little encroached upon by nervous matter that the name *aqueduct of Sylvius* would not be applied as a descriptive term were it not made necessary by usage in higher vertebrates. The aqueduct is produced laterally into a pair of spacious recesses, each of which occupies the interior of an optic lobe, while the general cavity communicates freely through narrower extensions with the third ventricle in front and the fourth ventricle behind (Fig. 1, *mb.*). The optic lobes are two thin-walled bodies of dome-like form, separated from each other by a conspicuous median furrow, and the pair taken together are somewhat broader than the base of the midbrain on which they rest. The anterior divisions of the cerebellum lie upon and partially conceal the optic lobes from the dorsal aspect. The base of the midbrain is a direct continuation anteriorly of the great fibre-system of the oblongata and metencephalon, showing but slight diminution in size.

The microscopical anatomy of the midbrain is really quite complicated, owing to the diversity of the terminations and connections which are established here. The base is a crowded highway between the different parts of the encephalon. The fibres of the optic nerve have their termination in the dorsal midbrain, the tectum mesencephali, with a nexus of intrinsic neurones and fibres of more distant origin associated with them. Finally, the aqueduct of SYLVIVS is bordered by nervous matter which is phylogenetically distinct from either the base or the tectum, and this has undergone special development at certain points as the nuclei of important motor neurones.

1. *The Tectum Mesencephali.*

The tectum mesencephali lies as an investing cap upon the central gray matter which surrounds the aqueduct of SYLVIVS. Its situation here is fraught with significance, for it represents an addition to the more ancient nervous structures made neces-

sary by the development of lateral eyes in the vertebrate phylum. The tectum embraces the central expansions and associated connections of the nerve-fibres having their origin as axones of the retinal neurones. Certain neurones of the tectum may, also, send their axones outward into the optic nerve. The whole complex is, in fine, the primitive visual centre.

The tectum of *Mustelus* does not approach the extreme degree of differentiation which RAMÓN Y CAJAL ('89, '91) has described from the optic lobes of birds, but it is practicable to distinguish three zones of structural elements: the layers of the superficial, the middle, and the deeper neurones, respectively (Fig. 21, *s.n.*, *m.n.*, *d.n.*). VAN GEHUCHTEN ('94) has described three zones from the optic lobe of the teleost, but these are not exactly equivalent to the layers noted here. His *couche moléculaire* appears to include both my superficial and middle layers; his *couche granuleuse* corresponds in position to my deeper layer; while his *couche des cellules épendymaires* is an inner zone which apparently does not include the central gray matter.

*a. Termination of the Opticus. Str. Medullare Profundum.*—

A great bundle of fibres may be traced dorso-posteriorly from each angle of the chiasma to the optic lobe, where it becomes dissolved through spreading over the surface. A section shows that the fibres in the outer zone lie parallel with the surface during some little part of the length of their course, and that they then pass downward into deeper parts of the tectum. Fine branches are given off in the regions occupied by the neurones of the middle and deeper layers, and many terminations appear to occur here. A certain number of fibres, however, pass to ever deeper levels, tending to become collected into bundles, and they finally blend into the stratum medullare profundum.

The stratum medullare profundum is a conspicuous feature of the deepest part of the tectum mesencephali. At the crown of the arch which the optic lobe presents in section, the fibres are seen as great horizontal bundles interrupted at almost perfectly regular intervals by small groups of vertical fibres. The

two lateral halves are united by a strong commissure just dorsal to the aqueduct of SYLVIVS. Fig. 20, *s. m. p.*, represents these features in a transverse section.

Traced laterally, the fibres of the stratum medullare profundum are found to pass into the base of the midbrain in two somewhat clearly marked divisions. The outer division takes a large number to the lateral surface (Fig. 20, *e. l.*); while a markedly smaller group passes downward nearer the median line for a ventral decussation (Fig. 20, *i. l.*). The inner division is composed of those fibres lying nearer to the central gray matter from the outset. Some of these have but a short course downward and outward, but the great mass of fibres continues near the median line as a series of intercrossing bundles which are destined to decussate ventral to the aqueduct of SYLVIVS (Fig. 20, *e. m.*, *i. m.*).

The fibre-system composing the stratum medullare profundum must be indeed important in the economy of the brain. Into this system we have traced fibres from the cord and oblongata, fibres from the optic nerve, and from the neurones of the tectum mesencephali itself. We will subsequently have occasion to point out that a great tract sweeps into it from the interbrain as a relay in the olfactory apparatus. Fibres are also present here from certain of the cranial nerves. All of these fibre-systems from diverse sources are to become related to the remarkable mechanism of REISSNER'S fibre. It is certainly evident that there are here every means for intercommunication between different parts of the nervous system, a switch-board, so to speak, of extraordinary possibilities; but to this subject we shall return further on.

*b. The Superficial Neurones.*—The outermost layer of the tectum mesencephali is characterized by the predominance of nerve-fibres and by the feeble development of its neurones. Receiving as it does the fibres of the optic nerve for their first expansion, we should hardly expect a high degree of nervous activity here. There are a few scattering nerve-cells present, however, (Fig. 21, *s. n.*). These are quite minute in size, lenticular in form, and are disposed with their long axes tan-

gential to the surface of the brain, as though squeezed into crevices between the mass of nerve-fibres. The internal organization of the cell presents no features which would mark it as having any degree of importance physiologically (Fig. 52, *s. n.*).

*c. The Middle Neurones.*—The neurones which lie in the middle layer of the tectum are characterized by their larger size and vastly greater numbers as compared with the outer region. In fact, the number is so great that in a section, the nerve-cells often appear superposed one over another, and the processes make a veritable tangle of interlacing branches (Fig. 21, *m. n.*).

The neurones of the level are to be distinguished from those of the deeper layer, on the other hand, both by their compactness and by their mode of branching, which is of the radiating type. The several processes of a nerve-cell spread out and branch freely in all directions, but they do not extend far away from their points of origin. A representative form is drawn in Fig. 22. There are always several dendrites, and these may arise either from the outer end or from the side of the polygonal cell-body. The branching begins quite near the origin, so that the size diminishes rapidly from the base outward. The dendrites of the outer extremity have their finest twigs penetrating the superficial layer of nerve-fibres. The dendrites arising from the sides of a cell interlace more largely with those of other neurones. The surface of a dendrite always bears an abundance of simple gemmules.

The axone pursues an irregular course, often spreading over a considerable horizontal area, but the general trend is ever toward the centre of the brain. It gives off a great profusion of collaterals as it proceeds, and the final termination is found at no great distance from the cell-body. There is here, then, an illustration of a cell of the GOLGI II type. The several ramifying axones lie in the region occupied by the cells of the deeper layer.

The nucleus is a rounded, centrally located body, filling the larger part of the mass of the cell. The cytoplasm holds a few tigroid-bodies of small size, an evidence of a low order

of metabolic activity in this type of cell. Fig. 52, *m. n.*, exhibits what details of internal organization are visible under the highest amplification.

The part which the neurones of this layer take in the physiology of the optic termination may be inferred with some degree of certainty. The dense tangle of dendrites just beneath the incoming optic fibres constitutes a large surface for purposes of reception. The spreading axones in the layer beneath afford, with the neurones there, a physiological nexus of some superficial extent, possible paths of association, if we choose to apply the term here. We will return to this subject in the following subsection.

*d. The Deeper Neurones.*—This layer is thicker than both the preceding ones put together. The neurones are less closely crowded than those of the middle layer, and they lie in groups between the bundles of optic fibres passing downward to the stratum medullare profundum (Fig. 21, *d. n.*).

The neurones which give character to this layer are long-drawn-out, the dendrites extending nearly to the external surface of the brain, and the axone reaching well toward the *limitans interna*. Fig. 23 shows a typical neurone considerably enlarged. The cell-body is spindle-shaped or oval in outline. From its outer end, a single stout dendrite proceeds straight toward the periphery. This dendrite branches but sparsely, and no branches are given off for some distance beyond the point of its origin. The several branches pass outward through the middle layer of neurones, and the most delicate twigs can be traced into the superficial layer of nerve-fibres. The whole dendritic series presents a top both tall and narrow, in strong contrast to the form assumed by the neurone of the middle layer. Gemmules are scattered over the branches, but they are conspicuous neither for their size nor their numbers.

There may be other minor dendrites arising from near the base of the cell, as shown in Fig. 23; but the axone always takes origin from a point opposite the principal dendrite. The axone is directed toward the *limitans interna*. It may be traced for some distance without any very marked diminution of size.

Many collateral branches are given off in its course, and the ultimate destination of the principal stem appears to be a bundle of fibres contributing to the stratum medullare profundum.

The body of the cell is so largely filled with the nucleus that often only the thinnest investing film of cytoplasm is exhibited. Six cells from this layer have their structural features shown in Fig. 53, and one of these has the thinnest enveloping cytoplasm found in this class. The nucleus of a cell is regularly oval in contour, holding one prominent nucleolus. The chromatic network is delicate and of small mesh.

The cytoplasm contains masses of tigroid substance which, in proportion to the actual magnitude of the cell, are relatively large in size. When the nucleus lies toward one end of the cell, the largest tigroids are found in the free extremity. The prevailing form of tigroid mass is triangular, and the several masses have a rather open arrangement.

From the form of the neurone just described, we should infer that it is adapted to the part of a conducting medium between the superficial and the deeper levels of the tectum mesencephali. The internal structure also indicates that it is characterized by no slight amount of metabolic activity. Evidently, then, there is here a nervous element of considerable importance in the economy of the midbrain.

VAN GEHUCHTEN ('94) has described the deeper neurones from the optic lobe of the trout (his *couche granuleuse*) as being without dendrites, and as sending their axones peripherally into the superficial levels. The character of this type of neurone in *Mustelus* certainly corresponds the more nearly with the conditions found in higher vertebrates, although much simpler of course, so that, in this respect at least, the selachian is seen to be in the direct phylogenetic line, while the teleost is divergent.

In the inner zone of the deeper layer of the tectum, at the level occupied by the numerous collaterals from the proper axones, there are to be found at intervals neurones of another character (Fig. 21). Such neurones are irregularly stellate as to general form, the dendrites and the axone radiating widely

from a polygonal cell-body. The office of this neurone may be to bring the collateral branches of the other and more numerous nervous elements into relationship. Fig. 54 shows a group of five of these cells, an unusually large number to find in so limited a field.

## 2. *The Central Gray Matter.*

The aqueduct of SYLVIVS is surrounded by a layer of nerve-cells and nerve-fibres representing the most archaic part of the brain, and quite properly termed the central gray matter (Figs. 20 and 21, *c. g. m.*). The greater part of this nervous matter has been supplanted or overshadowed functionally by more recent additions upon its outer surface, but certain well defined groups of neurones have retained their pristine importance through the character of their ultimate connections. These are, respectively, the roof-nucleus, and the nuclei of the oculomotorius and the trochlearis.

*a. The Roof-Nucleus.*—This is a collection of very large neurones lying in the roof of the aqueduct of SYLVIVS between the ependyma and the dorsal commissure of the stratum medullare profundum. The group has a considerable longitudinal extension, reaching from the anterior end of the optic lobes to near the juncture with the cerebellum. It is broken into two lateral halves by the median line. Fig. 20, *r. n.*, exhibits the entire nucleus; while Fig. 55 represents the distribution of the cells more in detail on the right side.

These neurones are the largest of any in the nervous organization of *Mustelus*. The size attained by the cell-body may be as great as  $60\ \mu$  in transverse diameter by  $100\ \mu$  lengthwise. The group, therefore, presents a very striking picture in the field of the microscope. The forms assumed by the cell-bodies are somewhat diverse, ranging from oval, through irregular outlines to a considerably elongated condition. The longer axis lies parallel, or nearly so, with the limitans interna.

In a thick section, the dendrites appear as two or three stout processes which push their way into the nervous matter dorsal to the group and are soon lost to view. Those cells

lying very close to the median plane send their axones to the opposite side; but the remaining members of the group, comprising nearly all of the cells, have their axones extending away from the mid-line. The axones from the several cells of the same side, together with the crossed axones, run laterally for a greater or less distance, turn anteriorly, and become associated into bundles which constitute a fairly well-marked tract (Figs. 20 and 55, *r. n. t.*). This tract extends forward to the anterior limit of the midbrain, where it unites with its fellow from the opposite side, and the united group of fibres emerges from the midbrain roof to penetrate the aqueduct of SYLVIVS as the fibre of REISSNER. The ultimate destination will be traced in a subsequent paragraph.

Those cells of the roof-nucleus lying in the posterior region have a different termination for their axones from the one just described. In this instance, the axones pass posteriorly, instead of anteriorly, and they take a course into cerebellum. The significance of this fact has been considered in Section V, Sub-section 5.

The cell-nucleus is a large, evenly rounded body, almost invariably eccentric in its position, sometimes, even, lying in what appears to be a special protrusion of the general cell-mass. The chromatin is distributed in the form of a reticulum of rather fine mesh which holds coarser granules at intervals. The nucleolus is evenly rounded and of conspicuous size. Many of the cells have two or even more nucleoli.

The cytoplasm, stained with methylen-blue, exhibits a minutely punctate appearance even under the highest amplification, due, chiefly, to the minute size and diffuse distribution of the tigroid substance. The tigroids are quite densely packed in the peripheral regions of the cell. In the field of the nucleus, the prevailing form of granule is rounded; farther away, the shape is a more elongated one, the long axis being tangential to the margin of the cell. Fig. 56 shows the details of cell-organization, NISSL staining.

When these cells are stained with iron haematoxylin, they exhibit what appears to be the equivalent of the perinuclear



reticulum of GOLGI (1900). We find the internal part of the cytoplasm exhibiting deeply stained, massive bodies, branching, and anastomosing with each other through more slender connections. The several individual masses are disposed in such a way as to give the appearance of enclosing the nucleus as with an open network. The bodies fade away as they enter the dendrites, and there is no appearance of their having communication with the exterior such as has been described by HOLMGREN ('99a, '99b). Fig. 57 represents the appearance of this series of structures.

It is doubtless necessary to await further researches in many distantly related fields before we attempt to pass final judgment as to the significance of the perinuclear reticulum, but the hypothesis noted by GOLGI (1900) is one which certainly deserves our consideration. The appearance presented by the network may be caused, not by solid bodies at all, but by a series of communicating canaliculi filled with a fluid which is deeply colored by certain stains. Such a reticular canal-system would probably take no part in the irritable life of the cell as such, but would function on a lower plane of purely vegetative character.

The neurones of the roof-nucleus come into intimate relations with the nerve-fibres of the stratum medullare profundum. The dorsal decussation between the opposite halves of the stratum carries a strong bundle of fibres across the median plane immediately above this group of neurones (Fig. 55, *dc. s. m. p.*). There are to be found here numerous instances of nerve-fibres emerging from the general bundle and terminating in arborizations near the bodies of the nerve-cells. Fig. 57, *ar.*, represents two such arborizations near the same cell. The character of the termination is exceedingly interesting. The axones are found to present a reticulo-vesicular structure throughout their whole length, the protoplasm apparently consisting of vesicles of several degrees of size united by a reticulum. Now as the axone approaches its termination, the reticulation becomes more pronounced, and the final arborization is seen to be essentially an expansion of the same thing. The ending is

simply a widely-spread, digitate reticulum. There are many thorn-like branches from all of the strands, and numerous anastomoses occur between the principal ones. Consult Fig. 57, *ar*.

The remarkable group of nerve-cells comprising the roof-nucleus has been variously interpreted, but its true relations were not discovered until quite recently. ROHON ('77) first described this collection of cells as the *Dachkerne*, a name applied, of course, from the position occupied by its paired members in the roof of the aqueduct of SYLVIVS. It was later recognized in the brains of various fishes, BURCKHARDT ('92) identifying it as the midbrain trigeminal nucleus. It has remained for SARGENT (1900) to show that not only is the roof-nucleus present in all vertebrates, but that it is part of a most interesting mechanism, the fibre of REISSNER ('60). REISSNER's fibre is a rod-like body lying in the central canal of the spinal cord, extending forward. It had come to be neglected entirely in recent years owing to the prevalent view that it merely represents a coagulation of the cerebro-spinal fluid. SARGENT (1900) demonstrated that such a view is erroneous, that REISSNER's fibre is a real structure, with a perfectly definite character and distribution, and, furthermore, that it is found in all classes of vertebrates, always extending from the posterior end of the *canalis centralis* to the anterior end of the aqueduct of SYLVIVS. He has also shown (1901) that the fibre represents, in the main, the closely fused axones of the cells of the roof-nucleus. The great number of neurones comprising the anterior field of the roof-nucleus send their axones into the aqueduct of SYLVIVS, as noted above, whence they pass backward as REISSNER's fibre through the extent of the fourth ventricle and the central canal of the spinal cord. Fine processes are given off to the nervous matter of the cord as the fibre proceeds.

An interpretation of the roof-nucleus and of REISSNER's fibre arising from it may now be attempted. In the next to the last paragraph, a nexus was traced between the fibres of the *stratum medullare profundum* and the neurones of the roof-nucleus. There are here, it is evident, the elements of a tract through which quite direct connections may be established be-

tween the somatic motor neurones of the spinal cord and certain sensory impressions, visual and olfactory, at least. The classes of impressions noted are carried through the stratum medullare profundum to the terminal arborizations which we have described near the cells of the roof-nucleus. The neurones of the roof-nucleus transmit such impressions through their axones, REISSNER'S fibre, directly to motor neurones at the several levels of the spinal cord. The apparatus of the roof-nucleus and REISSNER'S fibre, regarded as a thing apart, is advantageous to *Mustelus* because it is a path without relay, a short arc for motor reflexes between the eye and the olfactory organ, on the one hand, and the body musculature on the other. The giant size of the neurones of the roof-nucleus is doubtless the correlative of not only their long axones, but of their importance in the economy of the animal, as well. In ascending the scale of the vertebrate series, however, it will be found that this mechanism ever takes on a progressively less and less value, owing to the development of other means for attaining the same end.

*b. The Nucleus of the Oculomotorius.*—The nucleus of the III nerve lies ventral to the aqueduct of SYLVIVS (Fig. 58, *n. III*). This collection of neurones is sharply marked off from all surrounding nervous elements by the large size of its cells and by the greater intensity of stain with methylen-blue. The group extends antero-posteriorly for some distance.

The prevailing form of cell is oval, with two or three marked extensions of outline produced by the broadly triangular bases of the dendrites (Fig. 59). The axone is more slender by far than the dendrites; it is directed away from the *limitans interna*, taking the course of a sweeping curve.

The nucleus of the cell is evenly rounded in form, rather large as to proportionate size, and it has a central location. There is but a single nucleolus. The chromatin is distributed in a delicate network, the few interlacing strands visible being of great tenuity.

The cytoplasm is remarkable for the large size of its masses of tigroid substance, these bodies being visible as distinct things even under low amplification. The form of a tigroid is

almost invariably triangular. The base of the triangle lies toward the nucleus, the apex pointing in the direction of a dendrite. Those masses lying in contact with the nuclear membrane are somewhat broader, taking the form of a so-called nuclear cap. The size of mass decreases toward the periphery of the cell, those lying in the bases of the dendrites assuming a slender form. Reference may be made to Fig. 59.

The striking size attained by the masses of tigroid substance here is doubtless associated with the purely motor function of the III nerve, the fibres of which are the axones of these particular neurones.

*c. The Nucleus of the Trochlearis.*—ROHON ('77) fell into a curious error with regards the nucleus of the IV nerve. As is well known, the root of the trochlearis passes backward and crosses over to the opposite side, appearing dorsally in the furrow between the midbrain and the cerebellum. ROHON evidently sought for the nucleus of the nerve near its superficial origin, for he identified as such a group of cells on the border of the cerebellum.

The group of neurones constituting the nucleus of the IV nerve lies posterior and slightly ventral to the nucleus of the III nerve (Fig. 58, *n. IV*). The anterior end of the trochlear nucleus overlaps the posterior end of the oculomotor nucleus for a short distance.

The cells of this collection are, as compared with the cells of the oculomotor nucleus, decidedly smaller in size, and the general outline is more nearly triangular. The nucleus of the cell is relatively larger in proportion to the amount of cytoplasm. The chromatic network is so delicate as to be but faintly visible even under high magnification.

The masses of tigroid substance are few in number, relatively large in size, and wholly irregular as to form. There is a perinuclear zone of cytoplasm entirely free from tigroids. It often appears as though many of the tigroid masses are actually clinging to the limiting pellicula of the cell. Fig. 60 exhibits a condition typical for the cells of this group.

I really am unable to offer any explanation concerning the

marked differences to be observed between the tigroid-bodies of the trochlear and the oculomotor neurones, respectively. The contrast in both the form and the arrangement of the tigroids is quite evident. The distinction is a real one, not due to variation in the action of reagents, for I have several instances showing the marked contrast in one and the same section. A structural difference here is a noteworthy fact, since the two neurones are both of the somatic motor type, entirely equivalent morphologically.

### 3. *The Ependyma.*

The general character of the ependyma of the midbrain is represented in Fig. 21, *ep.*, while Fig. 61 illustrates the details of cell-organization. The outline of a representative cell is somewhat lance-like, the length four times the breadth, the pointed extremity touching the ventricle and the greatest breadth at a point further removed. The interior of the cell is occupied almost entirely by the nucleus. It is really difficult to detect any cytoplasm at all except in a small area at the base of the ependymal fibre. The observer has the impression forced upon him that most of the cytoplasm during the course of growth has passed over into the cell-process. The structure of the nucleus is reticulated to an almost extreme degree. Some strands of the reticulum are relatively coarse, but many of them are so tenuous as to lie almost beyond the capacity of the microscope.

The ependymal fibre takes a course which is almost straight during the first part of its length, but toward the outer limit of the central gray matter crooked turns occur, and branches are given off. The diameter of the process remains uniform throughout except for slight swellings which occur at intervals. The fibre terminates at the periphery of the brain.

The fact that the ependymal fibre becomes irregular and branches only after it leaves the central gray matter for the newer additions outside may have a phylogenetic significance, indicating that at one time the process had no farther course than the outer limit of this most ancient nerve-substance. But

it is also entirely possible that the phenomena in question are without such deep significance, having been caused by the greater number of obstacles in the path of the fibre as it grew through the outer levels.

#### 4. *Phylogeny of Midbrain Structures.*

The midbrain has ever been a stable part of the neural tube. Marked out early in ontogeny from the other brain-segments, the midbrain of *Mustelus* retains many features of organization which are really primitive in character.

The central gray matter is the most archaic of the midbrain structures, and the newer additions of the outer levels are derivable from it. The central gray matter is to be compared, both as to general functions and morphological topography, to the gray matter of the spinal cord before the latter has developed its specialized cornua. In a broad way, the ventral region of each is motor, and the dorsal part a series of sensory centres. The homology is most readily traceable in the ventral region. The neurones of the III and IV nerves are true somatic motor neurones, corresponding entirely to those of the ventral cornua of the cord.

The dorsal region of the midbrain has become more and more specialized as an optic termination. At a phylogenetically early period, the optic fibres grew backward from their original relations to establish terminations here. Probably the most primitive connection is the one with the giant neurones constituting the apparatus of the roof-nucleus and REISSNER's fibre. Through this means, the optic neurones were chained directly to the somatic motor neurones innervating the body musculature. Later, the midbrain roof became thickened by the wandering outward of neurones from the central gray matter, and by the development of new optic terminations associated with them. Thus has arisen the tectum mesencephali, an end-station which has remained important in the vertebrate series as a visual centre until secondary connections were established with the pallium. Hence the tectum is of great magnitude in the lower vertebrates, where the pallium is weak, but becomes

dwarfed in the mammalian brain in which there is an overshadowing development of pallial connections.

### 5. *Summary of the Midbrain.*

The tectum mesencephali of *Mustelus* receives practically all of the optic fibres, apparently only collateral branches being given to the interbrain. Three structural zones of the tectum are to be recognized: the superficial, the middle, and the deeper zones, respectively. The superficial layer has chiefly fibres, with a few minute, tangentially elongated neurones. The middle layer is composed of a densely crowded tangle of neurones of the GOLGI II type, the axones of which spread laterally. The deeper layer has neurones which send long dendrites into the outer levels, while their axones penetrate the stratum medullare profundum. Optic terminations occur in all of these layers. The structure of the deeper layer places the selachian more nearly in the direct phylogenetic line than the teleost.

The stratum medullare profundum receives optic fibres, axones from the tectum, fibres of the olfactory mechanism from relays in the thalamus, as well as fibres from posterior regions.

The central gray matter has become differentiated at certain points to form the roof-nucleus, and the nuclei of the III and IV nerves, respectively.

The roof-nucleus is a collection of very large neurones lying dorsal to the aqueduct of SYLVIVS, the axones of which form, ultimately, the fibre of REISSNER. Terminations of fibres from the stratum medullare profundum occur near the neurones of the roof-nucleus. The roof-nucleus and REISSNER's fibre constitute a direct path for motor reflexes between certain senses and the body musculature, involving the somatic motor neurones of the spinal cord. The senses thus mediated are, primarily, the olfactory and the visual, but the acustico-lateral and the general cutaneous systems may be represented also.

The neurones forming the nuclei of the III and IV nerves have the structure of the somatic motor neurones pertaining to the spinal cord and the oblongata.

Ependymal fibres extend through the entire thickness of the midbrain wall, branching but feebly.

## SECTION VII. THE INTERBRAIN.

The research of EDINGER, *Das Zwischenhirn*, ('92), presents an account of the fibre-tracts of the interbrain of Selachii and Amphibia as demonstrated by the WEIGERT method. It remains for me to add to the results of that work a description of the morphology of the neurones proper to the interbrain of *Mustelus*.

### 1. *The Thalamus.*

The thalami of a selachian are so small in proportion to the other parts of the brain (Fig. 1, *th.*) that certain of the older anatomists were thereby caused to overlook the interbrain entirely; see Section II. The small size of the thalamus is, I find, the expression of a low degree of organization. Several investigations have made it clear that the thalamus of a mammal has several well-defined thalamic nuclei. The thalamus of *Mustelus*, however, has remained in a condition of such primitive simplicity that it is not practicable to institute very strict comparisons between its neurones and those which are characteristic of higher forms. Before such comparison can be of much value, a study must be made of thalami having intermediate degrees of development.

It has seemed to me advisable to distinguish but two collections of neurones in the thalamus of *Mustelus*. One group represents a differentiation of the ancient central gray matter; this I have designated the nucleus strati grisei. The other collection is certainly the one from which the several geniculate nuclei of higher vertebrates have been derived; this I have called the nucleus geniculatus.

*a. The Nucleus Strati Grisei.*—As has just been mentioned, this collection of neurones represents a differentiation of the primitive central gray matter. The nucleus strati grisei has retained its original situation next the third ventricle (Fig. 24, *n. s. g.*). It forms a broad zone just within the limitans interna,



comprising something like one-fourth the thickness of the entire thalamus.

The neurones of this group are the largest of the thalamus. The cell-body has a polygonal form, the several diameters not greatly unequal. The dendrites radiate freely in all directions, but they are not very long. The nucleus of the cell has an eccentric position, causing the cytoplasm to appear massed on the side from which the chief dendrites arise. The chromatic substance is disposed in a few thin strands having thickened nodes. The entire amount of chromatin is not great, and so the nucleus presents a lightly stained appearance. The tigroid substance is limited almost entirely to that part of the cytoplasm having the greatest mass. Some of the tigroids are altogether irregular in form and are relatively quite large. Fig. 62 exhibits two neurones as they lie in place.

The nucleus strati grisei is the terminal station for those axones of the tractus strio-thalamicus having their origin in the general striatum. These sweep into the nucleus in bundles, and their terminations are to be noted between the constituent neurones (Fig. 24, *f. s. l.*).

The neurones of the nucleus strati grisei are, primarily, a relay in the olfacto-motor chain. The tractus strio-thalamicus terminating here is one of the links of that chain, as we shall point out in detail under Section VIII. The axones from the cells of the nucleus strati grisei pass backward into the base of the midbrain as the tractus thalamo-tectalis, and then sweep upward into the tectum to lie in the stratum medullare profundum. Here they are associated with other sensory nerve-fibres, as already noted in Section VI, and the entire group becomes related to the remarkable motor conducting path provided by the cells of the roof-nucleus and the fibre of REISSNER.

It is certainly not worth while, with the knowledge which we have at present, to attempt an extensive comparison of the nucleus strati grisei with the specialized thalamic nuclei of higher vertebrates. It seems fairly safe, however, to regard the nucleus rotundus and the nucleus magnocellularis as descen-

dents of this simple collection of cells found in the thalamus of selachians.

*b. The Nucleus Geniculatus.*—This nucleus is imbedded in the substance of the thalamus lateral to the nucleus strati grisei. It is separated from the neurones of that group and from the external surface of the brain by bundles of fibre-tracts. In transverse section, this collection of neurones appears as a broad band curving parallel with the limitans externa (Fig. 24, *n. gen.*).

The size of a neurone from the nucleus geniculatus is considerably less than that of one from the nucleus strati grisei, and the form is of the elongated instead of the radiating type. Fibres from the opticus leave that nerve to form a terminal zone on the periphery of the thalamus, and the dendrites of these neurones extend outward into this zone, while their axones take a course inward. The neurone, therefore, comes to be drawn out in a direction approximately at right angles to the limitans externa (Fig. 24, *n. gen.*). The cell-body is rendered somewhat elongated by the processes taking origin at its extremities. The interior of the cell is almost wholly occupied by the nucleus, leaving but a scanty amount of cytoplasm in the bases of the cell-processes (Fig. 63). The chromatin is in the condition of a fine reticulum. The tigroid substance is necessarily small in amount where there is so little cytoplasm, embracing only a few scattering granules.

Structurally considered, the neurones of the nucleus geniculatus are little specialized, remaining in an embryonic condition, so to speak. Their functional value is also of a low order. They are certainly of far less importance as an optic termination in the selachian than are their specialized representatives in the mammal. In *Mustelus*, only collateral branches are, evidently, sent to the nucleus geniculatus, the great mass of optic fibres sweeping backward to the midbrain for termination in the tectum. With the progressive evolution of higher vertebrates, the thalamic termination of the opticus appears to have become more and more important, leading to the corresponding differentiation of geniculate nuclei. Hand in hand

with the growing importance of the interbrain as a primary optic centre, however, there has been a related decline of the midbrain roof. And hence it is that the optic lobes of the fish appear so disproportionately large in comparison with the homologous parts of the mammalian brain.

2. *Epithalamus: The Nuclei Habenulae.*

The nuclei habenulae, or ganglia habenulae of authors, rise considerably above the level of the thalami (Fig. 1, *n. h.*), the pair meeting each other to form a conspicuously arched bridge across the third ventricle at its posterior end. The epiphysis springs from the middle of the arch. The left nucleus is a little larger than the right one, its margin extending slightly more anteriorly.

The nucleus habenulae is an important relay-centre, and so its structure exhibits many nerve-fibres taking various directions, between which there are neurones and supporting elements. The tractus olfacto-habenularis (Section VIII, 1, c) terminates here, and the neurones of the nucleus give origin to the tractus habenulo-peduncularis, (the bundle of MEYNERT, and the fasciculus retroreflexus, of authors).

A representative neurone is shown in Fig. 25. The size of the entire element is rather large. The cell-body tends to retain a rounded form, although diverted from this condition more or less by the thickened bases of the dendrites. The dendrites are some three or four in number, gnarled and irregular processes, branching only a few times, and extending far outward in every direction from their points of origin. The surface of a dendrite is roughened by nodal thickenings, knobs, and a few gemmules. The axone arises directly from the cell-body in all of the instances observed. Its course is traceable for only a short distance in a transverse section, since it soon turns posteriorly into the tractus habenulo-peduncularis. This important tract takes the usual course toward the base of the midbrain. Its termination occurs there in the nucleus interpeduncularis. The significance of the tract is to be interpreted as a part of the olfacto-motor complex, discussed more particularly in Section VIII.

### 3. *Hypothalamus: The Lobi Inferiores.*

The hypothalamus is very large in *Mustelus*, projecting far back beneath the midbrain; consult Fig. 1. Its large size is merely the expression of the unusual importance which is assumed by this part of the interbrain in selachians. Intrinsic neurones, and fibres from without are to be noted in numbers in both the infundibulum and the lobi inferiores.

The wall of the infundibulum exhibits neurones separated from each other by considerable intervals (Fig. 26). The cell-body is polygonal or elongated-oval in form. The dendrites are few in number. They spread widely, rarely branch, and pursue a nearly straight course.

*The Lobi Inferiores* are the most conspicuous features of the hypothalamus, a pair of great bulbous outpushings of the lateral wall of the infundibulum (Fig. 1, *l. i.*). These lobes are the seat of a crowded group of neurones, a fact which is doubtless the ontogenetic cause of their large size.

HERRICK ('92) has described several distinct nuclei from the lobus inferior (hypoarium) of the teleost, but I have found it impracticable to distinguish cell-groups in *Mustelus*. The neurones are disposed in a layer next to the *limitans interna*, the cell-bodies forming a closely-packed zone involving something like the inner fourth of the thickness of the wall (Fig. 27, *i. z.*). The dendrites are directed outward, forming, together with the nerve-fibres here, a fine tangle which presents the appearance of a molecular layer with general stains.

The form of a neurone is quite unlike that of any other found in the anterior divisions of the brain. It is not dissimilar to a widely spreading bush, the cell-body being the short stem, and the dendrites the top (Fig. 28). The dendrites are thick at their bases, they give origin to only a few branches, they taper gradually, and their tips usually reach almost to the *limitans externa*. The surface of a dendrite exhibits a multitude of spiny gemmules of various sizes.

The course taken by the axone depends upon the position of the neurone. A neurone lying in the roof gives off its axone

from the base of the cell, and the axone passes ventrally, branching profusely (Fig. 27). A neurone from the side-wall (Fig. 28) invariably has its axone emerging from the side of the cell, taking a course toward the *limitans externa* for a short distance, then branching in a T-shaped manner. The fibres thus formed run parallel with the surface of the brain, one turning into the ventral part of the lobus, the other pursuing an arcuate course out of the hypothalamus (Fig. 27, *f. b.*). Such a fibre is marked by varicosities at intervals, and it bears collateral branches (Fig. 28).

The internal structure of two neurones from the lobus inferior is given in Fig. 64. The figure also shows how closely these neurones are packed. The nucleus is only fairly large, and it is surrounded by a thick layer of cytoplasm on all sides. The chromatic substance is scanty in amount; it is distributed in a few thin strands. The tigroid masses are not numerous, and most of them are quite small, with just a few large ones distributed at irregular intervals in the peripheral region of the cell.

#### 4. *Supporting Elements.*

Associated with the many and crowded nerve-tracts characterizing the structure of the interbrain, there is to be noted a corresponding development of both neuroglia and ependyma.

A neuroglial element has a few stout processes radiating in every direction from the cell-body, often pursuing a markedly tortuous course. They ramify in an exceedingly complicated manner, the finest twigs interlacing to form a dense mat; see Fig. 29. Neuroglia is found in the nuclei of the interbrain, serving to support both the neurones and the terminal fibres occurring there.

Ependyma is found in all parts of the interbrain. The ependymal fibre always extends throughout the entire thickness of nervous matter, from the ventricle to the *limitans interna*. The fibre branches midway in its course, the several limbs often diverging considerably. The entire fibre-system bears a multitude of fine mossy processes. These features are shown in Fig. 30.

*5. Summary of the Interbrain.*

The thalamus is small in size and has remained on a low plane of differentiation. It is practicable to distinguish but two thalamic nuclei. One, the nucleus strati grisei, has become defined from the central gray matter for the reception of fibre-terminations, chiefly those of the tractus strio-thalamicus from the striatum; the axones of the nucleus give origin to the tractus thalamo-tectalis. The other thalamic nucleus, the nucleus geniculatus, receives collateral branches from optic fibres. It is wholly inferior to the tectum mesencephali as an optic termination, but it represents the specialized geniculate nuclei of higher forms.

The two nuclei habenulae do not exhibit great disparity in size. An olfactory tract, the tractus olfacto-habenularis, terminates here; the neurones of the nuclei give origin to the tractus habenulo-peduncularis.

The lobi inferiores are the seat of a crowded group of neurones, and the lobes are thereby given a large size. A neurone has a widely spreading dendritic top. Its axone branches in a T-shaped manner.

Supporting elements are strongly developed. The neuroglia is remarkable for the mat-like interlacing of its branches. Ependymal fibres often ramify to a striking degree; they extend through the whole thickness of the neural tube.

## SECTION VIII. THE FOREBRAIN.

The key to the understanding of the vertebrate forebrain was given by RABL-RÜCKHARD ('83) when he formulated the theory of the membranous pallium for the teleost. The extension of the generalization to other groups has been productive of results which fall into place in an almost schematic way. A quite remarkable series is given by the fishes. This series begins with a condition in the teleost where the entire roof of the forebrain remains non-nervous, and culminates in the dipnoid with a pallium having the essential morphological characters pertaining to all brains of a higher order.

The forebrain of *Mustelus* appears superficially to be somewhat divergent from the direct line of the series, owing to the absence of conspicuous external evidence of its bilaterality. The two striata are fused together into a solid basal mass; there is merely a broad and shallow furrow on the ventral side to mark their plane of contact. The pallium, while a thickened nervous plate as in far higher types of brains, is perfectly continuous between the right and left sides, and it is also confluent in the median plane with the striata below. These peculiarly compacted characteristics have been the source of no little controversy. STUDNICKA has attempted to show as one of the dicta of a series of papers ('94a, '94b, '95, '98) that the selachian forebrain stands entirely apart from that of all other vertebrates. His conclusions were drawn from studies on *Petromyzon*, and they appear to rest upon a misconception as to the extent of the tela choroidea superior. The fallacies of his views have already been pointed out by BURCKHARDT ('94c), and by RABL-RÜCKHARD ('94).

The lateral ventricles and the olfactory lobes of *Mustelus* really anticipate the two-lobed condition of higher forebrains in their essential characters. The lateral ventricles (Fig. 1) are derived from the outer angles of the third ventricle, and they pass the lamina terminalis some distance apart from each other. Their courses lie nearly parallel throughout. Each gives off two diverticula, the olfactory ventricle and a dorsal branch, respectively. The dorsal diverticulum, (Fig. 31, *p. v.*), is a short and narrow vertical cavity for the pallial eminence; see Subsection 4. This structure, while peculiar to the brains of certain selachians, is nevertheless of some comparative value, as will be evident further on.

The olfactory lobes are massive prolongations of the lateral angles of the forebrain. The primitive character of an olfactory lobe is exhibited by the sharply defined bulbus and tractus, and by the presence of the olfactory ventricle (Fig. 31, *ol. v.*). This is a slender cavity derived from the outer side of the lateral ventricle at the level of the pallial diverticulum.

The recessus neuroporicus of BURCKHARDT ('94a) is of

such interest as to deserve especial notice. It appears superficially as a well-marked depression in the median plane a little anterior to the pallial eminence (Fig. 1, *np.*). It is rendered even more noticeable during life by the penetration of blood-vessels here, owing to which fact ROHON ('77) called it the *foramen nutritivum*. This structure is the vestige of a neuropore. Its ontogeny was first described from the ganoid brain by VON KUPFFER ('90) as the *lobus olfactorius impar*. RABL-RÜCKHARD described its development in the selachian embryo ('93); and BURCKHARDT ('94d) has identified it in many other vertebrates. The recessus neuroporicus of *Mustelus* retains the character of an open passage in the adult animal (Fig. 31, *np.*), serving as a channel for blood- and lymph-vessels. It is accompanied by a pair of fibre-tracts, right and left, which take this primitive path from dorsum to base of the brain; see Fig. 31, *m. s. t.*

### 1. The Olfactory Lobe.

It is my purpose to devote a future paper to the entire olfactory apparatus of *Mustelus*, and so a detailed description of the olfactory lobe will not be given here. For the understanding of what follows, it will be sufficient to state that, in the bulbus, the olfactory neurones of the first order are chained to those of the second order through the usual tangles known as the olfactory glomeruli; and that the neurones of the second order, mitral cells, send their axones through the tractus to terminal stations described further on. Other neurones of the olfactory lobe, having a purely accessory value, need not detain us at present.

### 2. The Striatum.

The striatum is primarily a part of the olfactory apparatus, and its morphology must be interpreted with this fact in mind. Two groups of neurones have become defined from the general mass of the striatum for the especial reception of olfactory impressions. One of these lies next to the lateral ventricle, the epistriatum; while the other one is peripheral in its location, the nucleus postolfactorius. The structure of the principal



mass, or general striatum, will be considered after that of the epistriatum.

*a. Epistriatum.*—The epistriatum is a group of neurones lying ventral and lateral to the lateral ventricle (Fig. 31, *estr.*). It comprises something like the inner fifth of the entire thickness of the striatum. While not so sharply delimited from the outer levels as EDINGER ('96) has described for the reptilian brain, the epistriatum of *Mustelus* is readily distinguished from the general striatum by the smaller size and more closely crowded disposition of its neurones. The neurones are not arranged in any definite order; they are of the Golgi II type, sending their axones ventro-laterally into the striatum; refer to Fig. 32.

The cell-body of such a neurone ranges from triangular to polygonal in outline. There are three or four dendrites of only moderate length. These seldom branch except near their bases. They bear a very few gemmules and irregular knobs. The dendrites may extend indifferently in all directions, or they may lie tangential to the *limitans interna*.

The axone may arise from the cell-body, but in many instances observed it emerges from the thick base of a dendrite. It passes into the region of the general striatum, bearing short collateral branches along its whole length, and ultimately dividing into a widely spreading arborization between the neurones of the outer levels. Fig. 33 shows the external features of one of these neurones.

The internal structure of the neurone is shown in Fig. 65. The nucleus is seen to fill the greater part of the cell-body. It presents an oval form, and has chromatin disposed in a few relatively large masses, each consisting of a central clot with radiating streamers. There is a single nucleolus. The cytoplasm lies chiefly in the bases of the larger dendrites. Its tigroid-bodies are small in size, few in number, and irregular both in form and distribution. Judging from the structure presented by this neurone, it is not characterized by a high degree of metabolic activity.

The epistriatum is one of the nuclei for the termination of

olfactory neurones of the second order. Fibres also end here which have ascended in the tractus strio-thalamicus, and have crossed over in the anterior commissure. Some of the terminations occur near the bodies of the cells, but many of the fibres are to be traced to a narrow zone next the lateral ventricle into which the dendrites of the neurones penetrate (Fig. 32, *ol. f.*). Here the fibres give off branches which run parallel with the limitans interna. The significance of these terminations will be considered under the heading of the general striatum.

Comparing the description and figures given by JOHNSTON ('98a) for the ganoid brain, it would seem that the epistriatum is the more sharply marked in *Mustelus*. Although found in an animal ranking lower in the zoological series, the fact is doubtless a correlative of the more powerful olfactory organs which characterize the selachian organization.

*b. General Striatum.*—The median zone common to the pair of striata contains but few neurones. It is occupied chiefly by interlacing fibres of small calibre. The greater number of these are doubtless commissural, but in the more dorsal region there appear to be connections with the pallium.

The great mass of the striatum has neurones scattered through it without any order of arrangement (Fig. 31, *str.*). These neurones are never closely crowded, there usually being wide intervals between the cell-bodies. Their dendrites are very long, however, so that an interlacing plexus is given throughout the whole field. Fig. 34 will illustrate these features.

An individual neurone is shown in Fig. 35 drawn to a smaller scale than the other neurones of the striatum because its processes spread so widely. The cell-body may be rounded, oval, or polygonal in outline. There are numerous long and slender branching dendrites. Several dendrites often arise from a common thick stem which might almost be considered a part of the cell-body. A dendrite is noteworthy for the many little crooks which appear in its course, and also for the peculiarly spine-like gemmules which beset it. The latter feature is evidently characteristic of these neurones in fishes, as VAN GE-

HUCHTEN ('94) has noted their presence in the trout, and JOHNSTON ('98a) in the sturgeon.

The cell-nucleus has its chromatin disposed in slender, branching threads, and in minute granules distributed somewhat diffusely (Fig. 66). The cytoplasm forms a thick investment to the nucleus on all sides. Its tigroid masses are markedly larger than those found in the neurones of the epistriatum. The largest ones lie in the bases of the dendrites, and these have a triangular form. Other masses of smaller size and of more irregular shape are intercalated between the larger ones. Tigroids extend into the dendrites for a short distance, only.

The axone takes its origin directly from the cell-body, so far as observed (Fig. 35). It gives off collaterals during the first part of its length. The several axones descend to the base of the forebrain and run posteriorly in the tractus strio-thalamicus for ultimate termination in the thalamus; see Section VII. This conspicuous fibre-tract was described by ROHON ('77) as the *pedunculus cerebri*; by SANDERS ('86) as the *crus cerebri*; and by EDINGER in his earlier work ('88) as the *basale Vorderhirnbündel*.

The general striatum has the type of structure and the associations which are characteristic of motor centres. The large neurones, with their long and widely spreading dendrites, enter into a nexus with the axones derived from a purely sensory centre, the epistriatum. The latter receives, chiefly, impressions of the olfactory order. The neurones of the striatum are indirectly affected through the axones of the epistriatum, carrying, in turn, the nervous disturbance to the interbrain, whence a relay carries it to the great roof-nucleus of the mid-brain for direct connection with the neurones of the body musculature. The enormous olfactory organs of *Mustelus* indicate how important the olfactory sense must be in the economy of the animal, and observation demonstrates the large place taken by olfactory impressions in the location of food. The striatum is evidently the centre for motor reflexes, of which the sensory neurones chaining the olfactory organ to it constitute one arm,

and the neurones intervening between it and the body musculature comprise the other.

*c. Nucleus Postolfactorius.*—The nucleus postolfactorius is a collection of neurones at the ventro-lateral surface of the striatum near its anterior end (Fig. 31, *n. po.*). This nucleus is sharply demarcated from the general striatum by the closeness with which its neurones are arranged; Fig. 36 shows the morphology of five neurones as they lie in place. The peripheral zone is occupied by fibres, and also by the dendritic tips of the neurones themselves. The cell-bodies lie in a densely matted tangle of nervous processes just internal to the peripheral layer. A cell-body is somewhat larger than one from the epistriatum. The form ranges from pyramidal to elongated oval. The dendrites are rather few in number, relatively short, branching dichotomously once or twice. They are usually stout processes, gnarled, rough, and irregular, with but few true gemmules. Some neurones send their dendrites radiately in all directions; others take a more or less tangential course; still other are extended between the zone of nerve-fibres at the periphery and the striatum within. A conspicuously felt-like tangle is thus given by all of these interlacing dendrites.

The axone arises from one of the dendrites, so far as observed. It passes into the tractus olfacto-habenularis, coursing posteriorly along the ventral border of the forebrain for ultimate termination in the nucleus habenulae of the interbrain; see Section VII.

The internal structure of a postolfactory neurone is not of a pronounced motor type. The nucleus is always so large that it touches the periphery of the cell at one or more points, leaving the cytoplasm almost entirely in the bases of the dendrites. The chromatin lies in a fine reticulum. There may be two nucleoli. The tigroid substance is disposed in triangular or irregular bodies of smaller size than those noted for the striatum. These features are shown in Fig. 67.

The nucleus postolfactorius receives many olfactory fibres of the second order. A fibre entering for termination here is seen in Fig. 36, *ol. f.* This nucleus evidently holds a very dif-

ferent place in the olfactory apparatus from the epistriatum. The latter appears to be a sensory gateway to the striatum, while the postolfactory neurones enter into direct relations with the posterior regions of the brain.

### 3. *The Nucleus Neuroporicus.*

A group of neurones situated in the region of the recessus neuroporicus gives origin to a special bundle of the tractus strio-thalamicus, the *Medianbündel* of EDINGER ('88). I shall designate this group the *nucleus neuroporicus*. The neurones of the nucleus neuroporicus lie chiefly behind the external opening of the neuropore, just beneath the surface of what is really the most anterior part of the pallium. Other neurones of the same group are found at deeper levels, in the striatum, of course. The entire group is distributed, therefore, without regard to the anatomical boundaries which we seek to draw between the pallium and the striatum.

A sagittal section of the neuroporic nucleus stained by the GOLGI method exhibits a bewildering nervous tangle. The components of this plexus are the processes of the intrinsic neurones, and the terminations of the olfactory fibres which sweep over from the tractus. The nucleus is seen, then, to be an additional olfactory centre.

Two neuroporic neurones are shown in Fig. 37, exclusive of the maze of nervous processes in which they lie. The cell-body is large, the largest, in fact, of any found in the fore-brain. Its form is quite distinctly polygonal, the number of sides being determined by the number of dendrites. The dendrites are very thick at their bases, and they are some three to five in number. Each one soon breaks up into large branches. The length of a dendrite is relatively short. Its surface exhibits thickenings and minute knobs sparingly distributed.

The axone may arise from the cell-body, but in most instances its origin is traceable to the thick base of one of the dendrites. The several axones from each lateral half of the nucleus run anteriorly to the level of the neuropore, where they curve upon themselves to follow the course of that chan-

nel, forming the *Medianbündel* of EDINGER ('88); see Fig. 31, *m. s. t.* The median bundles, right and left, are thus carried posteriorly and ventrally beside the recessus neuroporicus toward the base of the brain. Here each blends with the part of the tractus strio-thalamicus taking origin from the striatum of that side, forming its central portion.

The course taken by the median bundle, curving forward as it does to lie beside the vestige of the neuropore, is certainly fraught with significance. This is probably an ancient route which was at one time quite direct, but the phylogenetic enlargement of the forebrain has carried the recessus neuroporicus and the seat of the neurones ever farther and farther apart.

The neurones of the nucleus neuroporicus probably function as an olfacto-motor centre, supplementary to the chief one represented by the general striatum. The relations of this nucleus to the pallium will be discussed under the following subsection.

#### 4. *The Pallium.*

The neurones of the pallium lie chiefly in what are called in this paper the *pallial eminences*; see Fig. 1 and Fig. 31, *p. e.* I have introduced the definitive term pallial eminence for the hemispherical roof of the dorsal diverticulum of each lateral ventricle (Fig. 31, *p. v.*). The earlier anatomists had observed the presence of these elevations in certain selachian forebrains, but their place in the organization of the pallium has not been recognized heretofore. A pallial eminence is the seat of a crowded group of neurones, and the elevated condition of the mass has probably arisen from the disproportionately rapid growth which occurs here.

The superficial zone of a pallial eminence is occupied almost exclusively by axis-cylinders, the significance of which will be noticed presently. The neurones lie in a crowded aggregate just within. Fig. 38 shows a representative group of these neurones. They are seen to embrace several varieties of form and size, all disposed without arrangement into definite layers.

*a. Neurones of the Tractus Pallii.*—The external features

of the largest variety of neurone of the pallial eminence will be seen by referring to Fig. 39. This type assumes a variety of guises, but it is characterized by its larger size and by the fact that its axone enters the tractus pallii. The cell-body of such a neurone ranges from broadly oval to distinctly polygonal in form. The dendrites are long and widely spreading processes, arising through thick basal masses at three or four almost equidistant points. A dendrite branches once or twice, dichotomously as a rule, and the terminal lengths become quite slender. Its surface is slightly roughened by minute gemmules. These are far less conspicuous, however, than the gemmules observed in the neurones of the striatum.

The internal structure of one of these neurones is shown in Fig. 68, *p. t. n.* The organization is markedly motor in type. There is an abundance of cytoplasm investing the nucleus on all sides. The nucleus is a sharply defined, central body, with a single nucleolus, and chromatin which is disposed in a condition strongly suggestive of a reticulum, although not actually appearing so. The tigroid-bodies are quite large in the region of the nucleus, the largest, in fact, of any tigroids found in the forebrain. More slender tigroids extend into the dendrites for some distance. In the cell figured, the axone exhibits a small axone-hillock of oval form.

The axone arises from the cell-body, (Fig. 68, *p. t. n.*), or from the thickened base of a large dendrite, (Fig. 39). It pursues a straight course, although one with many local sinuosities. The several axones of this class come to lie in the superficial zone, and they are gathered into a longitudinal bundle which lies as a broad cap on the neurone-aggregate of the pallial eminence (Fig. 31, *tr. p.*). This is the beginning of the tractus pallii. The pallial tract runs backward to the great posterior curve of the forebrain, where it dips ventrally to the base and enters the interbrain. Here it decussates and passes onward toward the oblongata. The tractus pallii is the *Mantelbündel* of EDINGER ('88).

*b. Associative and Commissural Neurones.*—A second type of neurone found in the pallial eminence is distinguished from

the preceding one by its associative or commissural value, and it is also readily recognizable by its smaller size (Fig. 40). The cell-body tends to retain a globular form. It gives origin to two or three dendrites which radiate from it at equidistant points. The dendrites are only moderately stout, and they are never of great length. They branch but a few times. Their surface is sparsely studded with small gemmules. The axone may terminate on the same side of the brain; or it may enter the pallial commissure, (Fig. 31, *p. c.*), for decussation, terminating in the opposite half. The neurone shown in Fig. 40 is an example of the commissural class.

The internal structure of a neurone of either the associative or the commissural type is drawn in Fig. 68, *as. n.* The nucleus is a subspherical mass, so large that it occupies practically the whole of the cell-body. The only cytoplasm distinguishable is that which composes the bases of the dendrites. The nucleus stains quite deeply, owing to the dense reticulum of chromatin which pervades it. The cytoplasm has only a few tigroids of small size, an evidence of a feeble degree of activity for this type of neurone.

*c. Cajal Neurones.*—Still a third type of neurone is clearly the representative of the *Cajal cell* which RAMÓN Y CAJAL ('91) described from the cerebral cortex of the rabbit, and which RETZIUS ('93), and VERATTI ('97) have designated after the name of the discoverer. CAJAL neurones have been observed in all of the higher vertebrates by various investigators, and their identification in the brain of *Mustelus* makes it probable that they are common to all groups.

A CAJAL neurone is drawn in Fig. 41. This neurone occupies a superficial position, just beneath the stratum of fibres noted above; refer to Fig. 31. The cell-body is an irregularly elongated oval, with its major axis horizontal. From its opposite extremities, thick dendrites arise which run more or less nearly parallel with the *limitans externa*. A dendrite does not have marked turns in its course. It gives off branches along its upper margin which ascend toward the surface of the brain, while a few branches are derived from its under side and pene-



trate to deeper levels. The dendritic surface bears small gemmules and larger bosses in considerable numbers.

The axone is a direct continuation of one of the dendrites. Its point of origin is indicated by the surface becoming smooth and the course more irregular. The axone continues to hold a course tangential to the *limitans externa*, and it terminates through a few small branches at no great distance from its point of origin. This type of neurone is evidently purely associative, linking together areas not widely separated.

Structurally, the CAJAL neurone is somewhat peculiar (Fig. 69). The tigroid substance is collected into a few lumps of relatively large size. These are disposed irregularly in the great masses of cytoplasm which lie lateral to the nucleus. The nucleus is eccentric in position, leaving but a thin pellicle of cytoplasm on one of its sides. The chromatin is grouped into a few strands having conspicuously thickened nodes at intervals.

*d. General Considerations on the Pallium.*—The pallium of the selachian is really a primitive representative of the stem giving origin to the pallia of amphibians, reptiles, birds, and mammals. The continuity of its two halves, contrasted with the two-lobed condition of the higher type, has caused many writers to rank the selachian pallium as a divergent branch. The correctness of the view set forth in this paper will appear when the significance of the relations which exist between certain neurones of *Mustelus* have been considered.

It has been shown that the ventral border of a lateral ventricle is the seat of one olfactory termination, the epistriatum. The epistriatum tends to become extended round the side of the ventricle toward the pallium. Axones from the marginal neurones of this olfactory centre enter the pallium, thus serving to link that region indirectly with the olfactory organ. Besides this source of impressions, the olfactory centre of the nucleus neuroporicus radiates an influence to the pallium, of which it is really a part. The pallium of *Mustelus*, therefore, is seen to have a general association with the olfactory mechanism.

It has been shown by EDINGER ('96) that the special palial olfactory conducting path characteristic of higher verte-

brates appears for the first time in the brain of the reptile. Both EDINGER and HERRICK have also shown that the first sense to thus enter the field of consciousness is the olfactory one. The pallium of the selachian really anticipates the reptilian olfactory connection, although, of course, in a much simpler way. In *Mustelus*, we therefore find a quite primitive condition represented.

So far as we may be permitted to interpret morphological facts, the pallium of *Mustelus* would appear to be a long-distance motor centre of the olfactory apparatus. Other olfacto-motor centres there certainly are in abundance. Both the general striatum and the nucleus neuroporicus contribute motor neurones to the tractus strio-thalamicus; while the nucleus postolfactorius sends a tract to the nucleus habenulae. These centres obtain connection with posterior regions only through relays in both the interbrain and the midbrain. The pallium, on the other hand, sends its tract directly through the base of the interbrain toward the nuclei of the great nerves of the oblongata. The tractus pallii, therefore, gives the olfactory sense an additional hold on the nervous system, a series of connections which cannot obtain, of course, in those fishes with membranous pallia.

The phylogenetic development of the pallium of selachians would thus appear to be the outcome of the great dependence which these fishes place upon the olfactory apparatus in the search for food. In higher vertebrates, as the olfactory sense becomes linked to the pallium through stronger bonds, and as other senses make pallial connections, one after another, this part of the brain takes on functions of an ever higher value. In *Mustelus*, there is merely an anticipation of pallial possibilities.

#### 5. *Supporting Elements.*

Both neuroglial and ependymal elements are present in the forebrain of *Mustelus*.

Ependyma is found radiating from every part of the lateral ventricle, and its characters are nearly uniform for the several regions. The ependymal cells have their nuclei situated at

slightly different levels, and so a broad zone next to the ventricle presents chiefly nuclei. The shape of the cell-body is influenced by the position of its nucleus, of course, but the broadened part is usually not directly in contact with the ventricle. The ependymal fibre runs straight outward from the cell-body, as a rule, and it reaches entirely to the *limitans externa*. It does not branch, its size remains nearly uniform, and its course is only slightly irregular. It bears a greater or less profusion of delicate, mossy twigs of short length. The inner portions of two ependymal elements are shown in Fig. 42.

Neuroglia is found in the several parts of the forebrain where nerve-cells are grouped in numbers. While the specific forms assumed by neuroglial elements exhibit considerable diversity, all are referable to but one type. From an irregular cell-body, numerous fine processes extend in all directions for a short distance, branching profusely as they proceed. The ultimate twigs are of quite minute size, and hence it is that the whole presents a characteristically mossy appearance. Fig. 43 illustrates the features of a representative specimen.

#### 6. *Summary of the Forebrain.*

A fairly well-defined epistriatum is present, receiving olfactory and other terminations. Its neurones are of the GOLGI II type, sending their axones into the striatum, in the main. The axones from marginal zones enter the pallium.

Neurones with widely spreading dendrites are arranged in open order in the striatum. Their axones enter the tractus strio-thalamicus for termination in the thalamus. The striatum appears to be an olfacto-motor centre.

The nucleus postolfactorius is a densely crowded group of neurones. Olfactory fibres terminate here, and the derivative axones form the tractus olfacto-habenularis.

A group of large neurones in the vicinity of the recessus neuroporicus gives origin to the median portion of the tractus strio-thalamicus. This paired tract accompanies the neuropore for some distance. The nucleus neuroporicus is a third olfactory centre.

The pallium has its two halves fused in the median plane. Its most important region is the pair of pallial eminences. Each of these has a special extension of a lateral ventricle. The neurones of a pallial eminence are not arranged in layers, but it is practicable to recognize three distinct forms: (1) The neurones of the tractus pallii, the largest variety, their axones comprising the tractus pallii. (2) Commissural and associative neurones, the axones of which are distributed in the pallium itself, a special decussation of commissural fibres occurring in the median plane. (3) CAJAL neurones, lying tangential to the limitans externa.

The pallium of *Mustelus* is regarded by the writer as a primitive representative of the stem giving origin to the pallia of amphibians, reptiles, birds, and mammals. It anticipates the olfactory connections of the reptilian brain. The tractus pallii is interpreted as giving the olfactory sense a hold on the nervous system in addition to that provided by the epistriatum and striatum, and the neuroporic and postolfactory nuclei. The phylogenetic development of the pallium of selachians is believed to have been the outcome of the great dependence placed upon the olfactory sense by these animals.

#### SECTION IX. GENERAL SUMMARY AND CONCLUSION.

Special problems relative to the several parts of the brain have already been discussed in the foregoing pages; while summaries have been placed at the close of each of the sections. There yet remain for consideration a few topics of more general scope growing out of the study as a whole. Before proceeding to these questions, however, it will be desirable briefly to review the most important results which have been obtained.

##### 1. *General Summary.*

*The Oblongata* of *Mustelus* has become only slightly divergent from the structural plan of the primitive neural tube.

The ventral cornu of the spinal cord is continued into the oblongata as the nucleus of the VI nerve, and as the scattered commissural and tract-neurones of the *formatio reticularis*.

The viscerosensory system has had annexed to it a complex of peripheral sense-organs. The communis system which results from this union is represented by components of the VII, IX, and X nerves. The lobus vagi is the centre of the system. Fewer fibres enter the fasciculus communis than in either the teleosts or the amphibians.

The visceromotor nucleus gives origin to the motor fibres of the V, VII, IX, and X nerves. The axones enter their nerves chiefly through the medium of the fasciculus longitudinalis dorsalis. The nucleus receives impressions radiated from the lobus vagi.

The general cutaneous nucleus is the homologue of the dorsal cornu of the spinal cord. General cutaneous fibres, components of the V, IX, and X nerves, terminate in both the substantia gelatinosa and the deeper part of the nucleus. Many fibres of the system enter the spinal V tract for ultimate distribution in the spinal cord.

The tuberculum acusticum is phylogenetically young. It may have been derived from the structures of the dorsal cornu. Fibres of the acustico-lateral system terminate in the tuberculum acusticum. These are components of the VII, VIII, and X nerves. Neurones are present in the tuberculum acusticum of the molecular, granular, and PURKINJE types, equivalent morphologically to those of the cerebellum.

*The Cerebellum* is relatively large in *Mustelus*. This fact is to be interpreted from the strong development of the sense of equilibrium in the animal. The structural plan of the cerebellum is the same as that characteristic of higher vertebrates, the differences being due to greater simplicity of detail.

The evidence is for the origin of the cerebellum, in the phylogeny of the vertebrates, as a fused outgrowth of the pair of tubercula acustica. The organ represents a specialization of that part of the oblongata forming the original terminal station for the acustico-lateral system.

*The Midbrain* appears to have its organization arranged contributory to the roof-nucleus. This is a group of giant neurones, the axones of which enter into and very largely compose

the fibre of REISSNER. The roof-nucleus and REISSNER's fibre, together with the motor neurones of the spinal cord, provide a direct path for motor reflexes between certain senses and the body musculature. The senses thus mediated are, primarily, the olfactory and the visual, but the acustico-lateral and the general cutaneous systems may be represented also.

The stratum medullare profundum is an important highway into which there are traceable optic fibres, axones from the tectum mesencephali, fibres of the olfactory apparatus, and fibres from posterior regions. Fibres emerge from the stratum to terminate near the cells of the roof-nucleus.

The tectum mesencephali receives practically all of the optic fibres in *Mustelus*. Three zones of neurones are recognizable in the tectum, with optic terminations in all of them. The deepest of the three layers has a more generalized structure than the corresponding zone of the teleost.

*The Interbrain* is the seat of several important relays between the forebrain and the posterior brain-segments.

The thalamus is but slightly differentiated. Only two thalamic nuclei are recognizable. The nucleus strati grisei receives fibres, chiefly from the tractus strio-thalamicus; its axones give origin to the tractus thalamo-tectalis. The nucleus geniculatus receives collateral optic terminations. It is wholly inferior as an optic centre to either the tectum mesencephali of *Mustelus*, or to the specialized geniculate nuclei of higher forms.

The two nuclei habenulae are not greatly unequal in size. The lobi inferiores are the seat of a crowded group of peculiar neurones.

*The Forebrain* is regarded by the author as anticipating the forebrains of higher vertebrates in many respects. A fairly well-defined epistriatum is present, the axones from which enter both the striatum and the pallium. The striatum is an olfacto-motor centre; its axones enter the tractus strio-thalamicus for termination in the thalamus. An accessory bundle of the tractus strio-thalamicus is derived from the nucleus neuroporicus. An additional olfactory centre is provided by the nucleus postolfactorius.

The pallium has its neurones grouped, without arrangement into layers, chiefly in the pallial eminences. Three varieties of neurones are to be distinguished. The pallium receives impressions radiated from the adjacent olfactory nuclei; it therefore anticipates the olfactory connections of the reptilian and higher brains. The tractus pallii, arising from the pallial neurones, is regarded as giving the olfactory sense a quite direct connection with posterior regions.

## 2. *Conclusion.*

To one who has read this far, it must be evident that there is a most remarkable structural similarity between the brain of *Mustelus* and the brains of higher vertebrates. The results obtained by me do not bear out the conclusions of SZCZAWINSKA ('98) relative to the very low plane occupied by the selachian neurones; see Section II, 2. The neurones of *Mustelus* are, of course, simpler in their external morphology, and their architectural relations are of a far less complicated order, yet it is none the less true that they anticipate the conditions found in higher vertebrates in all important particulars. Such a fact is certainly the more remarkable when the great differences in the scale of general organology are taken into account. The fact can only be interpreted to mean that the nervous system of the primitive vertebrate had its essentials of organization well defined before the divergence of the several phyla occurred. A brain of the type presented by the selachian of to-day has not become sufficiently specialized during the lapse of time entirely to mask the ancestral characteristics. The brain of one of the higher vertebrates embodies many modifications of the original plan, wrought in the course of its gradual evolution. These alterations may even become more conspicuous than the primary structures upon which they have been superposed, and it is only through comparisons with a less differentiated condition that we can hope to distinguish the new from the old.

A comparative study of the several brain-segments of *Mustelus* is productive of some results that might not have been

anticipated. The cerebellum is marked by an organization out of all proportion to that of adjacent regions, an organization, moreover, far more highly differentiated than is presented by the cerebellum of either the amphibian or the reptile. The oblongata, on the contrary, has retained the plan of structure of the primitive neural tube without the intervention of profound changes. It is due to this fact that homologies between the oblongata and the spinal cord are so readily traced in this animal. A more extreme degree of simplicity is found in the interbrain, the thalamus having such a slight differentiation as to make comparisons between it and higher thalami somewhat difficult. Finally, the forebrain is far in advance of the forebrains of other fishes. Contrast the membranous pallium of the teleost or the ganoid with the nervous pallium of *Mustelus*, which, as has been pointed out in the preceding pages, anticipates the olfactory associations of higher brains to a noteworthy degree.

These illustrations clearly point to an underlying principle. The organization of the brain is the expression of the adjustment which has constantly taken place between the race of animals and the stimuli to which they have been subjected. This relationship between nervous organization and peculiarities in the environment is such a close one that the degree of development of the several parts of the brain may be very unequal indeed. And hence it is that the cerebellum of *Mustelus* is so highly organized, for this is the correlative of the powerful swimming capacity of the animal, requiring an adequate mechanism of equilibration. The forebrain, with its luxurious development of neurones, has arisen in connection with the large place occupied by olfactory impressions in the *Selachii*.

Morphological data in neurology must necessarily provide the foundation for all physiological work, but it is none the less important that morphological facts should have the check of experimental evidence wherever this is possible. Nowhere is there to-day a more urgent need for careful observations of this character than in the group of the fishes, where nervous processes are of such a simple order as to introduce relatively few



complications. THORNDIKE ('99) has made at least a beginning in this field for the teleosts. This observer placed a screen with but one opening across the course in which *Fundulus* desired to swim. He found that after several repetitions the animal "learned to get out." Here, it would seem, there was a true memory of previous activities in the absence of any nervous pallium at all, a very suggestive fact in connection with the interpretation placed in the present paper upon the pallium of *Mustelus*. An extension of the scope of experimental work on the fishes will certainly prove fruitful for comparative neurology in so many ways that the writer feels impelled to bespeak a larger place for this kind of work in our investigations.

Since the promulgation of the neurone concept of WALDEYER in 1891, no work has demanded more critical attention than that on the ultimate fibrillar structure of the nervous system, studies with which the names of APÁTHY, BETHE, and NISSL will ever be connected. An investigation of neuro-fibrils obviously lies beyond the bounds set for the present research, and observations concerning them in *Mustelus* must await another opportunity for expression. In the meantime, I would join with the protest made by A. MEYER ('99), PARKER (1900), and VERWORN (1900) against the tendency to elevate the results of specific methods into an exclusive dogma. Although spoken from a different vantage-point, the words of GOLGI (1900) may well be quoted here: "The knowledge which we possess, either anatomical or physiological, is not yet such as to permit us to interpret with certainty the greater number of the facts discovered, much less to attempt doctrinal constructions of a high order on the functional mechanism of the nervous elements."

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## SECTION XI. DESCRIPTION OF THE FIGURES.

All of the figures have been drawn with the aid of the camera lucida. A uniform scale of magnification could not be adopted because of the wide range in the sizes of the neurones. In order that comparisons may be facilitated, the scale of diameters of the drawing as reproduced is given in the description of each figure. The orientation is accurately maintained in all of the drawings, the dorsal parts being uppermost as the figure appears on the plate.

### REFERENCE LETTERS.

- a. f.*—Ascending fibre  
*a. l. f.*—Acustico-lateral fibre  
*aq.*—Aqueduct of SYLVIVS  
*ar.*—Terminal arborization  
*as. n.*—Associative neurone

- ast.*—Astrocyte
- ax.*—Axone
- ax. h.*—Axone-hillock
- b. f.*—Basal nerve-fibre
- bg. f.*—BERGMANN'S fibre
- bv.*—Blood-vessel
- cb.*—Cerebellum
- cb. cr.*—Cerebellar crest
- cb. inf.*—Inferior lobe of the cerebellum
- c. f.*—Communis fibre
- c. g. m.*—Central gray matter
- ch.*—Chiasma
- c. n.*—Commissural neurone
- dc. s. m. p.*—Decussation of the stratum medullare profundum
- d. n.*—Deeper neurones
- e. l.*—External division of the lateral ramus of the stratum medullare profundum
- e. m.*—External division of the median ramus of the stratum medullare profundum
- ep.*—Ependyma
- estr.*—Epistriatum
- ext.*—Limitans externa
- fb.*—Forebrain
- f. c.*—Fasciculus communis
- f. l. d.*—Fasciculus longitudinalis dorsalis
- f. s. t.*—Fibre of the tractus strio-thalamicus
- g. c. f.*—General cutaneous fibre
- g. c. n.*—General cutaneous nucleus
- g. l.*—Granular layer
- hy.*—Hypophysis
- III.*—The oculomotorius
- i. l.*—Internal division of the lateral ramus of the stratum medullare profundum
- i. m.*—Internal division of the median ramus of the stratum medullare profundum
- inf.*—Infundibulum
- inf. v.*—Ventricle of the infundibulum
- int.*—Limitans interna
- IX.*—The glossopharyngeus
- i. z.*—Inner zone
- l. i.*—Lobus inferior
- l. v.*—Lateral ventricle
- l. vg.*—Lobus vagi
- mb.*—Midbrain
- m. f.*—Median nerve-fibres, longitudinal bundle
- m. f'.*—Median nerve-fibres, transverse bundle
- m. l.*—Molecular layer



- m. n.*—Middle neurones
- m. s. t.*—Median bundle of the tractus strio-thalamicus
- n. g.*—Neuroglia
- n. gen.*—Nucleus geniculatus
- n. h.*—Nucleus habenulae
- n. III.*—Nucleus of the oculomotorius
- n. IV.*—Nucleus of the trochlearis
- np.*—Recessus neuroporicus
- n. po.*—Nucleus postolfactorius
- n. s. g.*—Nucleus strati grisei
- obl.*—Oblongata
- ol. f.*—Olfactory fibre
- ol. v.*—Olfactory ventricle
- op. f.*—Optic fibre
- p. c.*—Pallial commissure
- p. e.*—Pallial eminence
- p. l.*—Layer of the neurones of PURKINJE
- p. t. n.*—Neurone of the tractus pallii
- p. v.*—Ventricle of the pallial eminence
- r. lat. X.*—Ramus lateralis vagi
- r. n.*—Roof-nucleus of the midbrain
- r. n. t.*—Tract of the midbrain roof-nucleus
- s. m. p.*—Stratum medullare profundum
- s. n.*—Superficial neurones
- sp. V.*—Spinal V tract
- str.*—General striatum
- t. a.*—Tuberculum acusticum
- t. c. p.*—Tela choroidea posterior
- t. c. s.*—Tela choroidea superior
- th.*—Thalamus
- t. n.*—Tract-neurone
- tr. cb. s.*—Tractus cerebello-spinalis
- tr. p.*—Tractus pallii
- v. m. f.*—Viscero-motor fibre
- v. m. n.*—Viscero-motor nucleus

# PLATE VI.

*Fig. 1.* Median sagittal section through the brain of an adult *Mustelus*. The right lateral ventricle of the forebrain is indicated in broken outline. Natural size.

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*Fig. 3.* Structural elements from the formatio reticularis on the right side of the oblongata. The commissural neurone (*c. n.*) sends its axone across the median raphe. The upper neuroglial cell (*ng.*) has its longer axis extended in the radius of the oblongata. The GOLGI method,  $\times 230$ .

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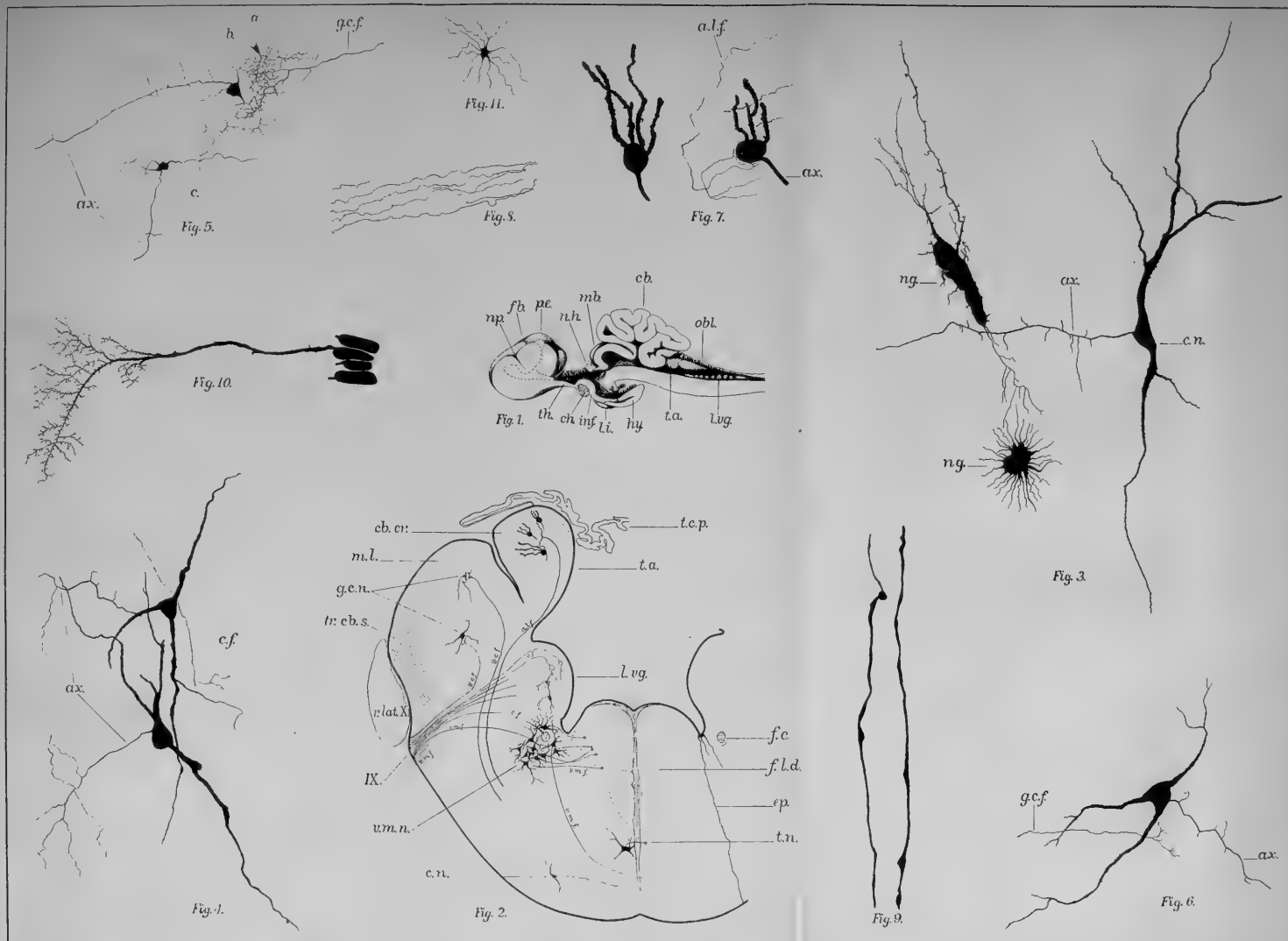
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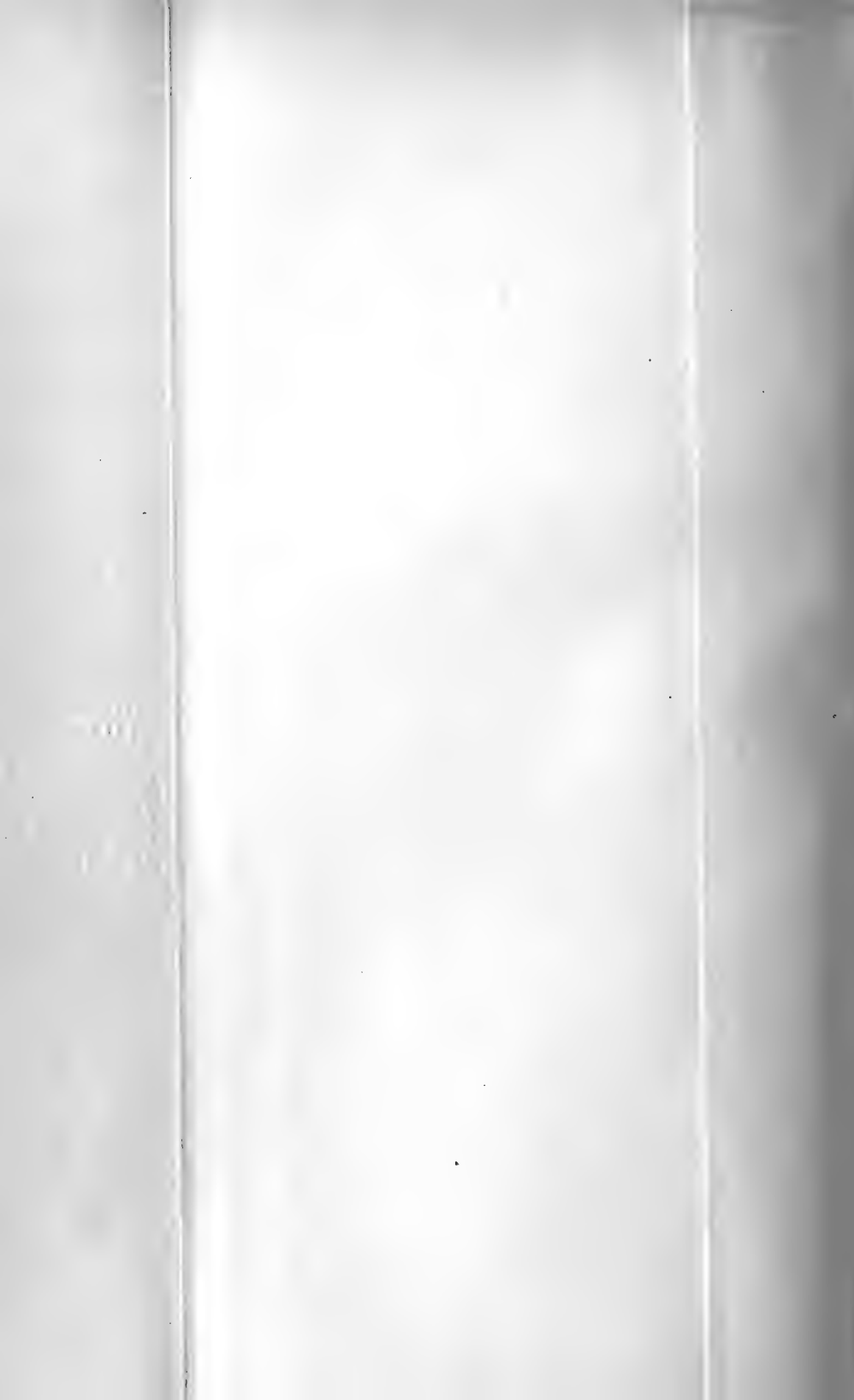
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*Fig. 69.* CAJAL neurone from the lateral part of a pallial eminence. The NISSL method,  $\times 1120$ .









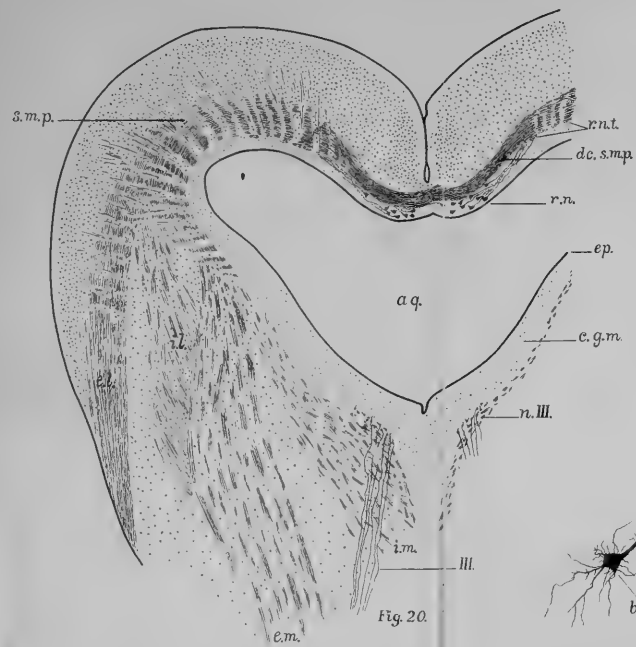
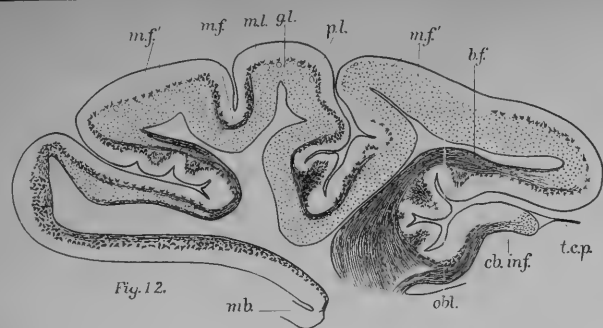
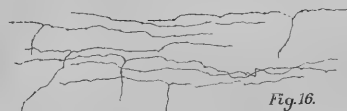
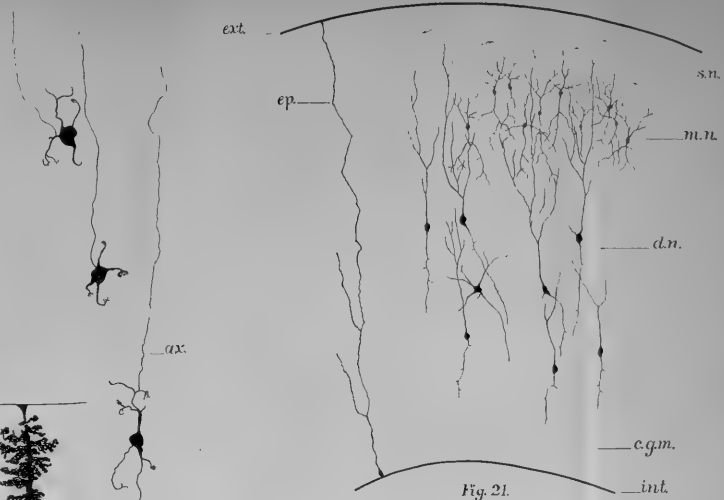
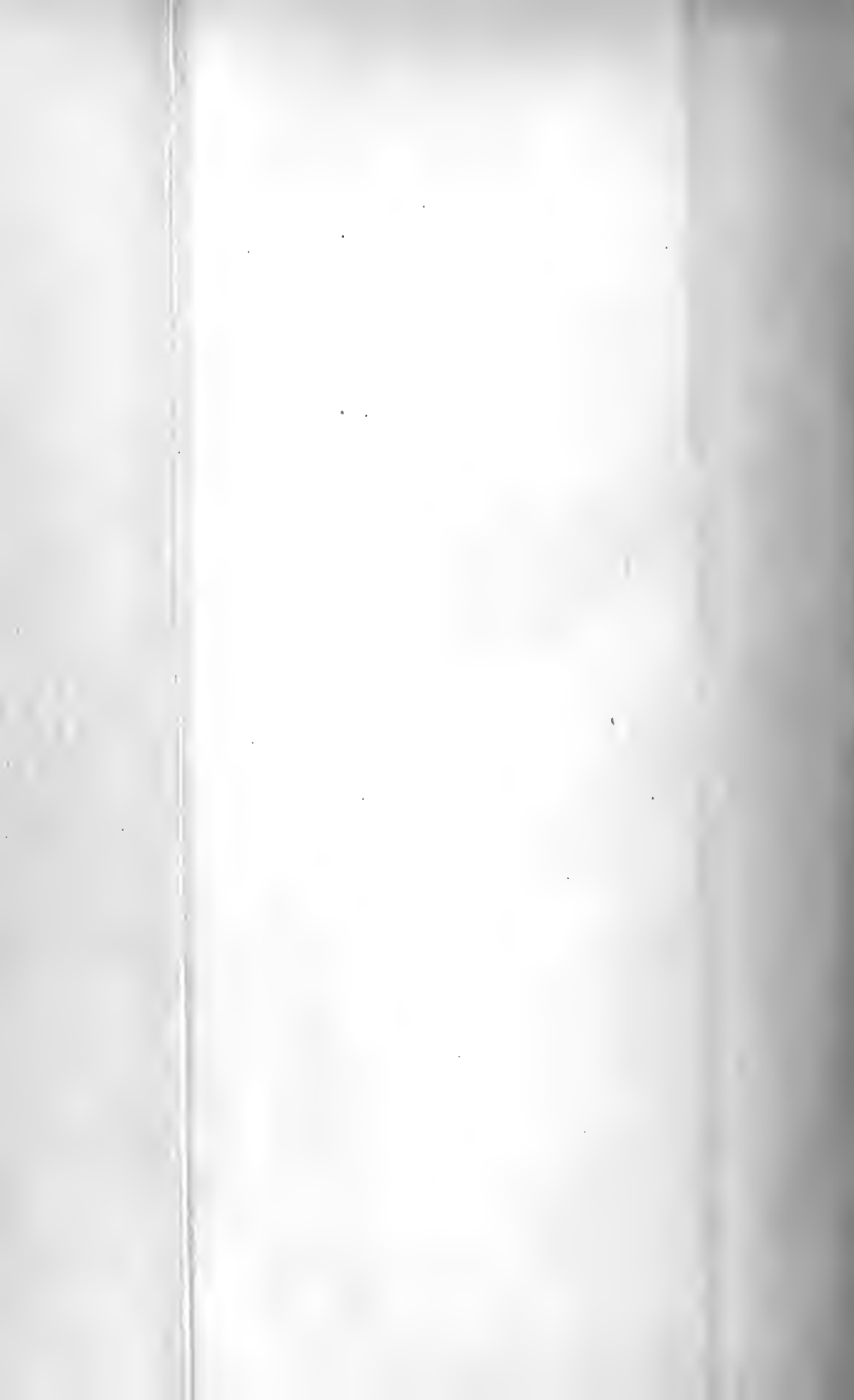
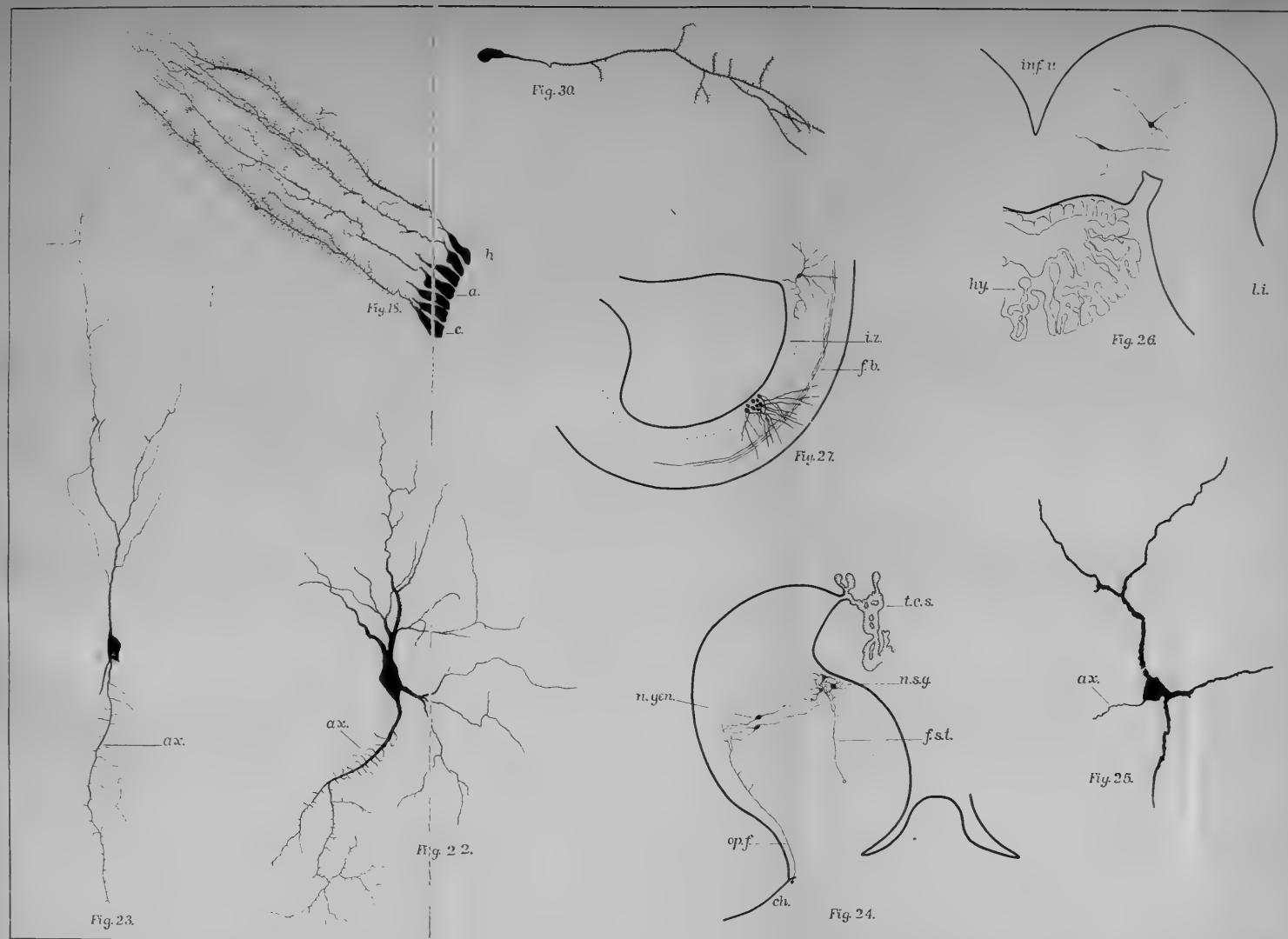
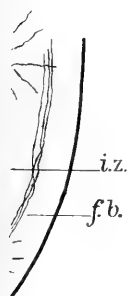


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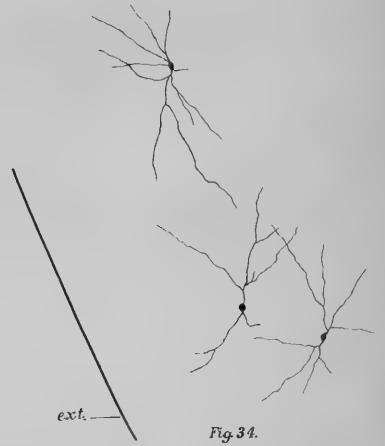
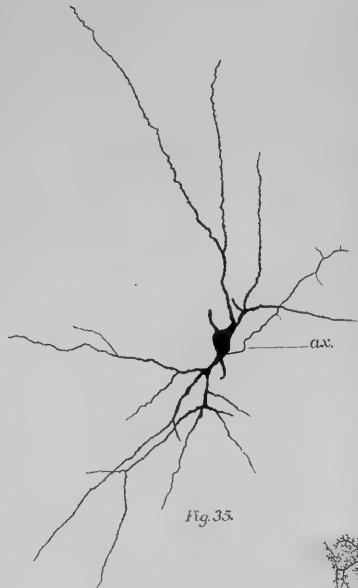
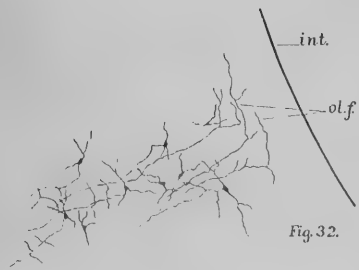
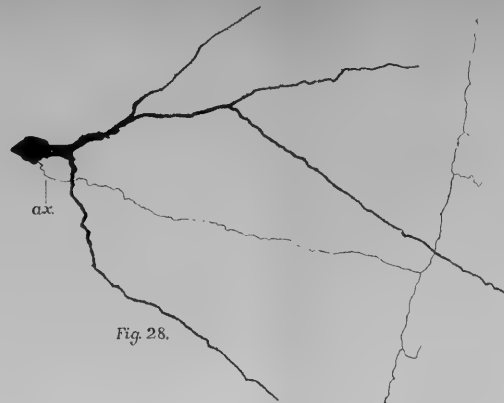
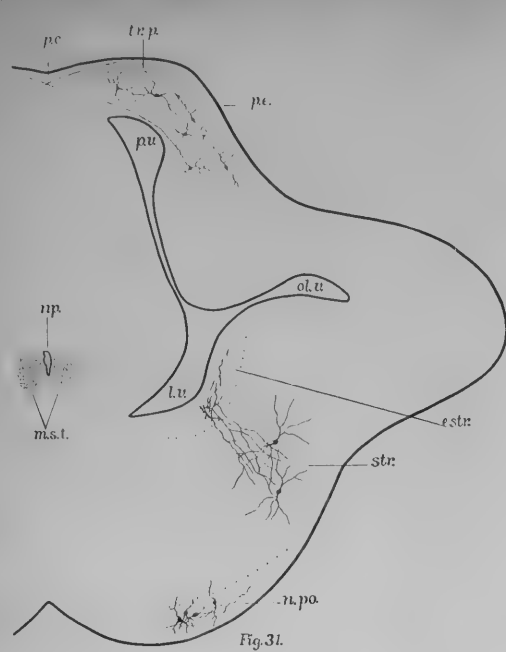




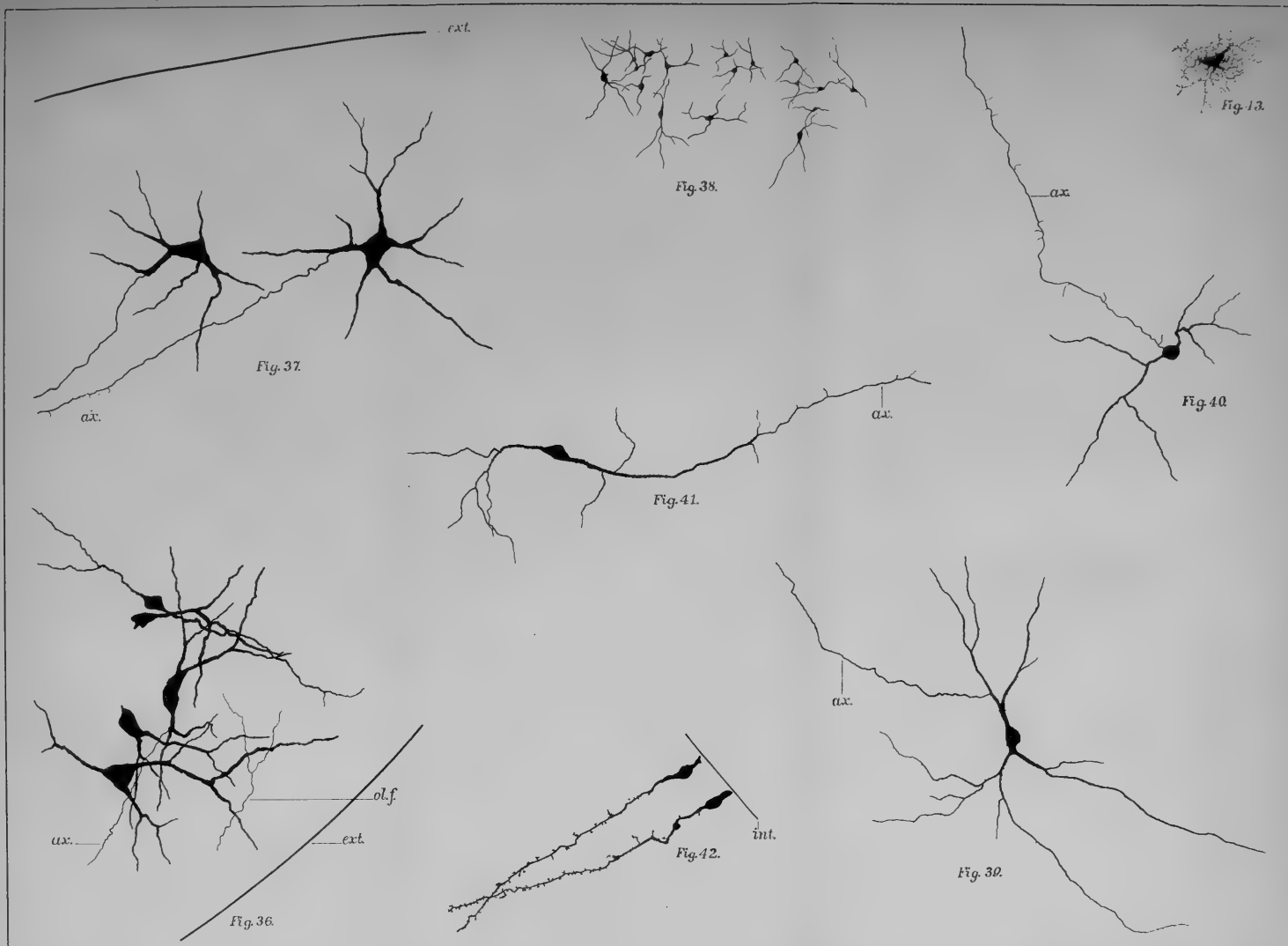
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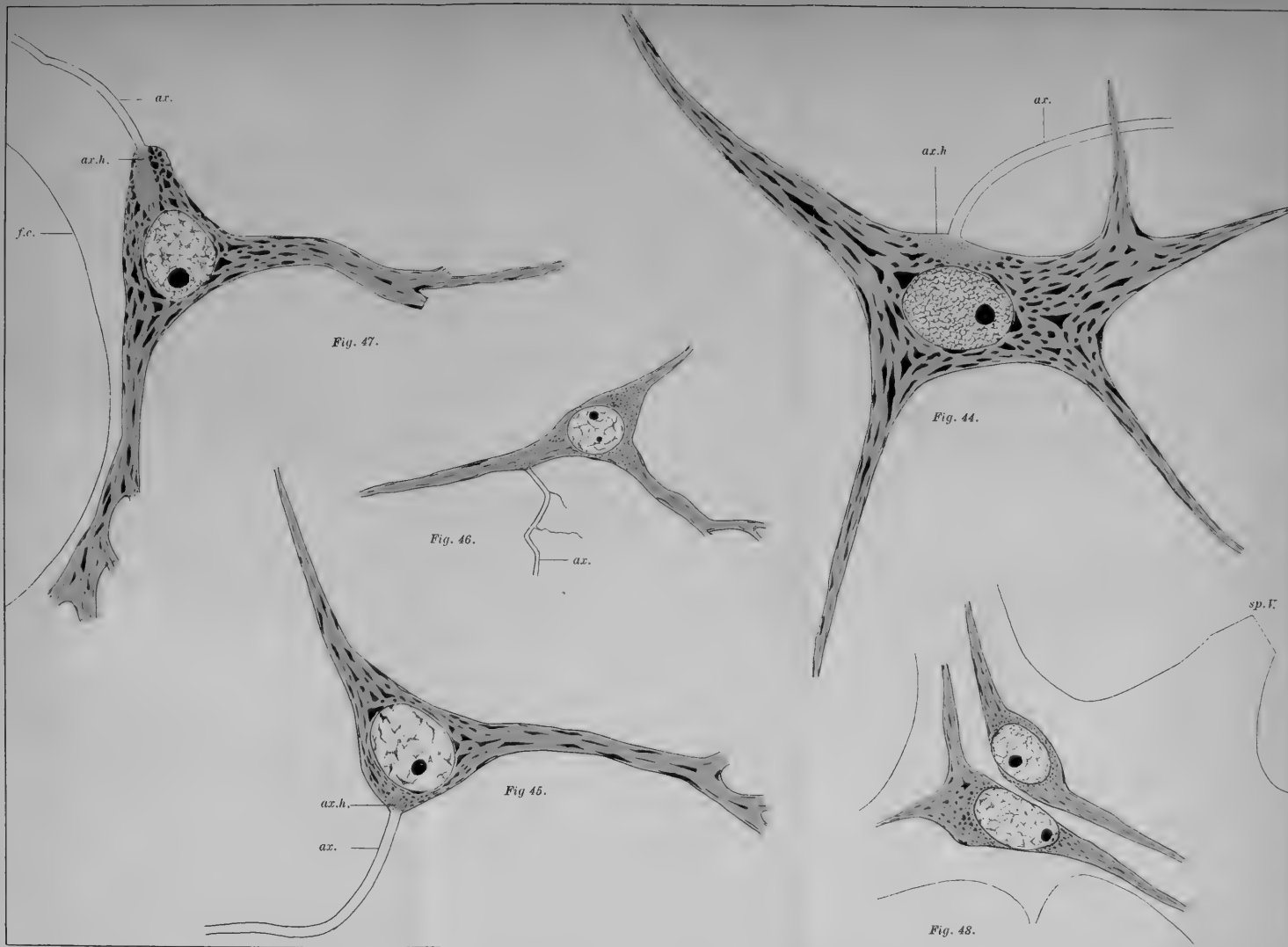


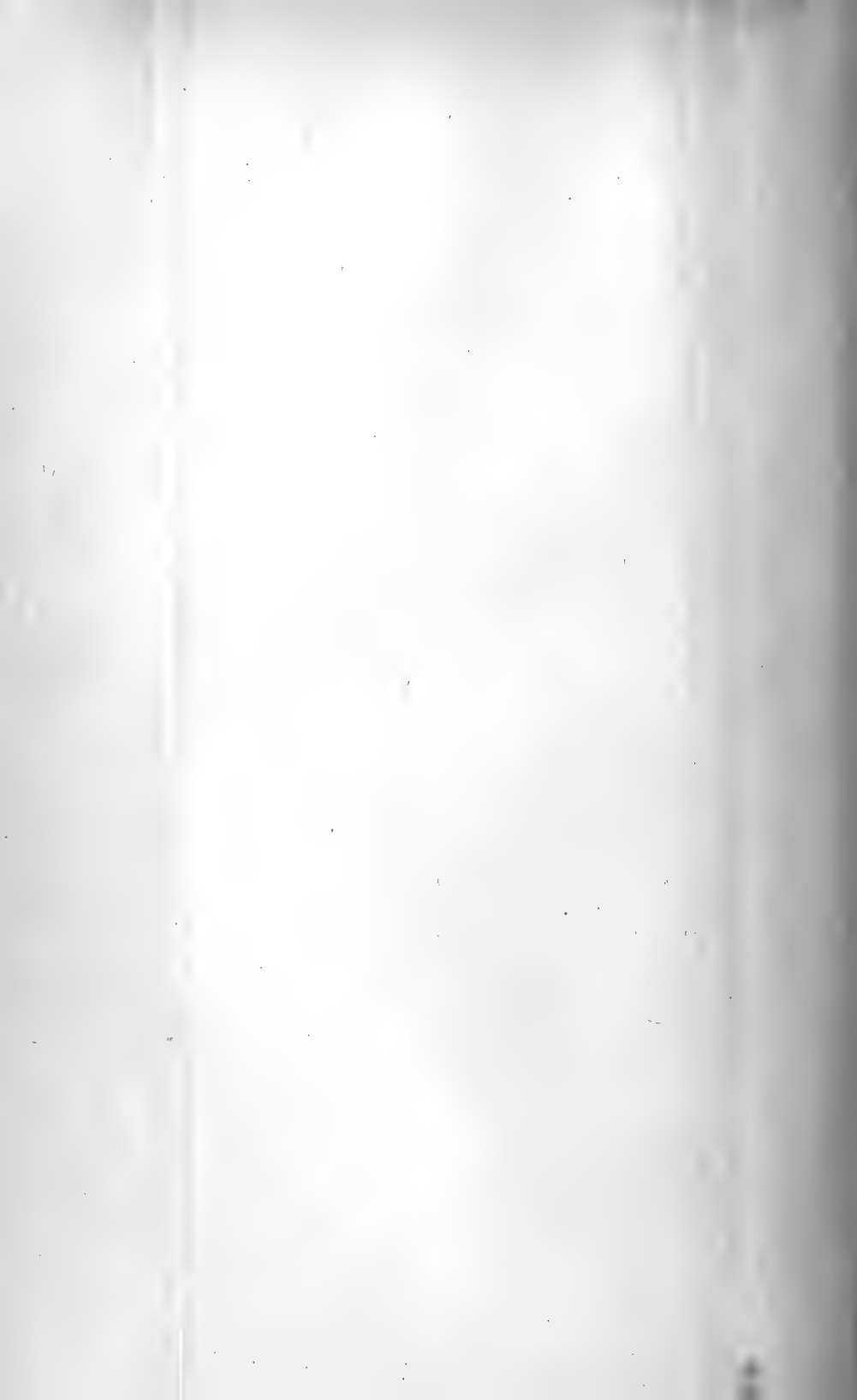


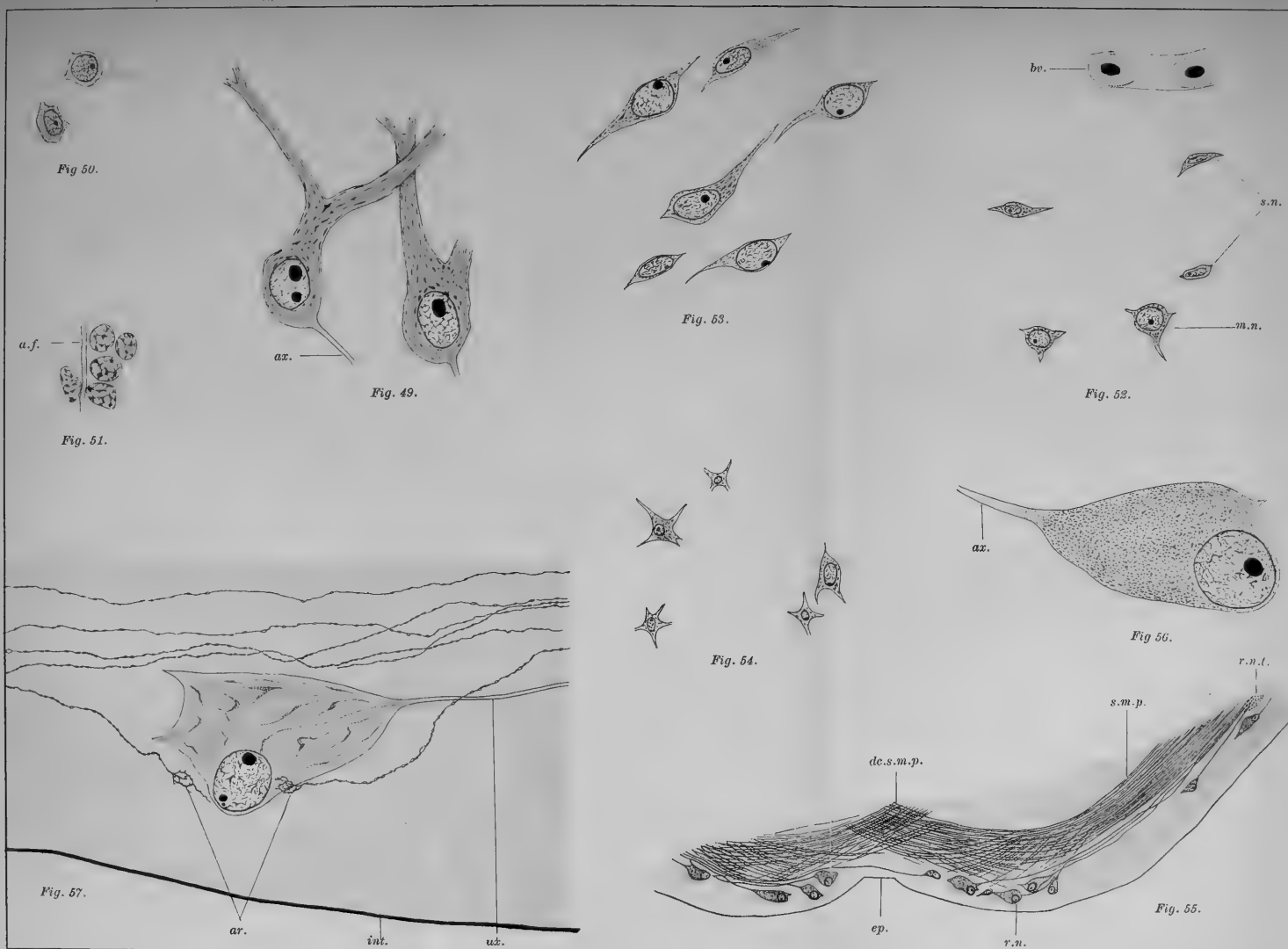














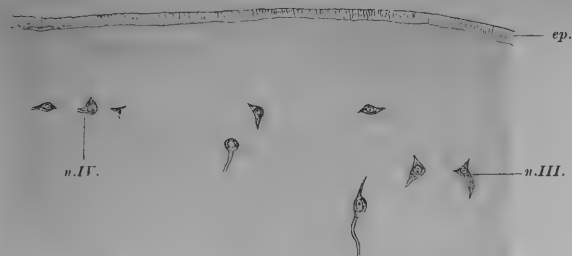


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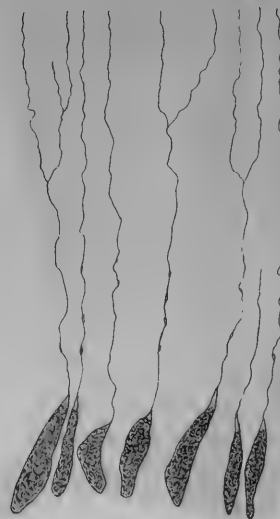


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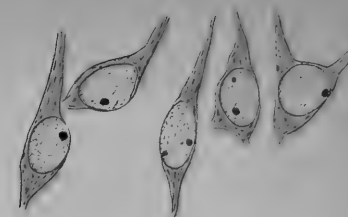


Fig. 67.



Fig. 60.



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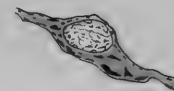


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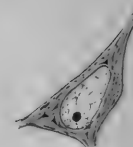


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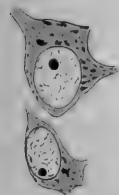


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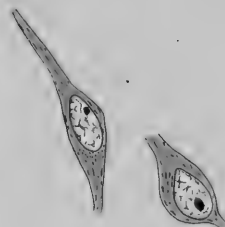
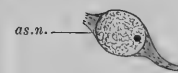


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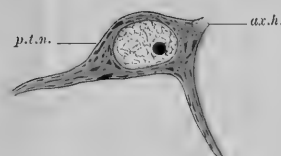


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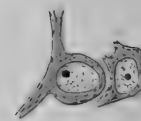


Fig. 64.



THE  
JOURNAL OF COMPARATIVE NEUROLOGY.

THE CRANIAL NERVES AND CUTANEOUS SENSE  
ORGANS OF THE NORTH AMERICAN  
SILUROID FISHES.<sup>1</sup>

By C. JUDSON HERRICK.

With Plates XIV—XVII.

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## INTRODUCTION.

Among the multitudes of interesting problems which are suggested by the study of the literature upon the fishes, few are of greater interest or of more far reaching significance than those centering about the diverse kinds of cutaneous sense organs among these types. A great step in advance was marked by MERKEL's discovery that these sense organs can be referred to two chief types, each with many varieties: viz. (1) the terminal buds, "End-knospen," similar in structure to the taste buds of the buccal cavity, and (2) the neuromasts, or organs of the lateral line system, "Nervenhügel," characterized by the presence of pear cells or specific sensory cells shorter than the others of the sensory epithelium and resembling in structure the hair cells of the organs of the internal ear.

Several of the recent students of nerve components among the Ichthyopsida have brought forth more or less convincing evidence that these two structural types can likewise be distinguished in their innervation, the terminal buds being supplied by the communis system of nerves and the neuromasts by the acustico-lateralis system. The reader is referred to the works of STRONG, ALLIS, KINGSBURY, COLE, JOHNSTON, HOUSER and



the present writer, among others (see the appended bibliography) and to the article "Cranial Nerves" in the second edition of Wood's Reference Handbook of the Medical Sciences (Vol. III, now in press) for the point of view regarding the nerve components from which the present study takes its departure.

No types known to me offer so many advantages for the study of this problem as the North American cat fishes, for these fishes possess both types of sense organs in exceptional abundance, diversity of forms and extent of distribution over the skin and they are moreover entirely without scales. The embryological method appears to be the most favorable avenue of approach; but believing that studies in development should be preceded by a thorough knowledge of the adult structures involved, I have undertaken a preliminary study of the cutaneous sense organs and their innervation. Finding the accounts in the literature often contradictory and always incomplete on points of greatest importance from this point of view, this work has grown into greater proportions than at first anticipated, and this must be my apology for presenting so large a mass of detailed descriptive matter, much of which is after all but a repetition of what others have found before me.

The nerves and sense organs of *Ameiurus catus* have been incidentally referred to by ALLIS ('89 and '97); the lateral line canals and their nerves have been more fully described by COLLINGE ('95); and this species has been monographed from several different points of view by WRIGHT, McMURRICH, MACALLUM and McKENZIE ('84). WRIGHT's account of the nerves and sense organs is the most complete and satisfactory and is characterized by a keenness of morphological discrimination which stands out in pleasing contrast to much of the descriptive work on the nervous system of the fishes. His account of the trigemino-facial ganglionic complex, while very incomplete, lays a good foundation for a thorough understanding of the components of these nerves. It is upon this foundation that the present contribution is based, my prime motive being the determination of the exact relations between the several types

of cutaneous sense organs and the terminal nuclei within the medulla oblongata to which these organs are related.

The topography of the chief nerve trunks having already been given by WRIGHT and the chief morphological features of their central termini by KINGSBURY, I shall here confine myself to the points of greatest value to the theory of nerve components; viz., the exact courses of the components through the V + VII and the IX + X ganglionic complexes and the exact peripheral relations of the communis and lateralis components of these nerves. The motor nerves will detain us in only a few cases and the orbital nerves have been fully described by my pupil, Mr. WORKMAN ('00). *Ameirus melas*, JORDAN and COPE, is the species most carefully studied and the microscopic examination of transverse sections through the whole body of the adult fish stained by the WEIGERT process is the method chiefly relied upon. Three specimens were sectioned transversely. The descriptions and illustrations following are all based on the left side of one of these specimens unless express statement to the contrary is made.

The details of the method in the case of this specimen are as follows: A small adult was hardened for 27 days, until fully decalcified, in FLEMMING'S stronger fluid. After five months in cedar oil it was embedded in paraffin and cut transversely into serial sections 13  $1.3\ \mu$  thick as far back as the middle of the dorsal fin. The sections fixed to the slide with MAYER'S albumen were mordanted in ERLICKI'S fluid over night, stained in KULTSCHITZKY'S acid hæmatoxylin 24 hours and decolorized in a mixture of equal parts of saturated solution of lithium carbonate and 1% solution of ferricyanide of potassium.

The work will be divided into two parts, (1) the description of the nerves and (2) the account of the cutaneous sense organs. As our interest in Part I centers largely about the innervation of the sense organs, it will be necessary in this place to anticipate briefly a few points which are treated more at length in Part II. The organs now under consideration, as indicated above, fall into two great groups in correlation with their nerve supply, which I have termed the communis and the acus-

tico-lateralis systems respectively. Those of the former system, the terminal buds, are, so far as I have observed, all alike and similar also to the taste buds of the buccal mōcosa save that they are somewhat larger and their nerve fibers are more heavily medullated. The acustico-lateralis system includes the organs of the internal ear (not considered in the present contribution), the organs of the lateral line canals and the pit organs, of which in *Ameiurus* there are two types; viz large pit organs and small pit organs. The large organs evidently correspond to those so often described in the literature under the name pit organs, as in *Amia*, *Gadus*, *Menidia* and many other teleostean fishes. They are not numerous, probably less than fifty on each side of the body in the specimens of *Ameiurus melas* which I have studied, while the small pit organs are very abundant indeed. The organs of the acustico-lateralis system are collectively termed neuromasts and their structure is considered more in detail in Part II.

## PART I. THE CRANIAL NERVES.

### I. THE TRIGEMINO-FACIAL COMPLEX.

It has long been recognized that the trigemino-facial complex of siluroids is much more intricate than that of most other teleostean fishes. STANNIUS mentions as an additional difficulty in *Silurus* a peculiarity which has embarrassed our work on *Ameiurus* also; viz., the fact that the fiber characters of the different components are much less marked than in most other fishes. Nevertheless STANNIUS was able to give ('49, p. 25) a very exact description of the central connections of the V + VII roots of *Silurus*.

Of the two fish types whose components I have previously studied in detail, *Menidia* exhibits the trigemino-facial roots and their ganglia in an almost digrammatic simplicity which we may well regard as primitive, while *Gadus* presents the same components arranged according to the same general scheme, but crowded closer together so that the relations, though discernable with precision, are much more difficult to make out. This process has been carried still farther in *Ameiurus* and all of the

ganglia have been fused into a single mass, the limits of whose component ganglia cannot always be determined with exactness. The roots are arranged in the same way as in the other fishes, but the sensory members of the complex have been so greatly enlarged as to obscure the relations still further by their mutual crowding. The enlargement is due in part (i. e., so far as concerns the general cutaneous component) to the enormous size of the head of the cat fishes and the correspondingly large cutaneous surface to be innervated. But the lateralis and especially the communis systems are likewise greatly enlarged, due to the fact that the pit organs and terminal buds, with which nearly the whole surface of the head is abundantly supplied, are also innervated from this complex, the communis root supplying the terminal buds scattered over the trunk also. But however much the peripheral relations of these nerves may be influenced by the presence and distribution of these sensory organs, it remains true that the roots and ganglia maintain the strictly typical relations presented by the less highly specialized fishes.

### 1. *The motor roots.*

The relations of the motor V and motor VII roots conform to previous descriptions and agree with my previous findings in *Menidia*. They are not indicated on the projections, but are represented in the series of transections (Figs. 4 to 8). The peripheral relations of these nerves have also been fully worked out and I confirm the work of my predecessors save in a few particulars, which will be mentioned beyond.

### 2. *The general cutaneous root.*

The fibers of this root enter the spinal V tract, and terminate in the general cutaneous nucleus, a convenient term introduced by HOUSER ('01, p. 95) for the entire terminal apparatus of the general cutaneous system. The spinal V tract is ill-defined along the mesal aspect and is accompanied by cells on this side which represent a part of the terminal nucleus, or substantia gelatinosa, as in human anatomy. Following the

usual order of description, we shall trace the root outward from the brain.

Just before emerging from the oblongata it receives the motor V root (Fig. 8) and runs out dorsally of the communis root, internal to the dorsal lateralis root and ventrally of that portion of the geniculate ganglion from which the r. lateralis accessorius arises, all of these being crowded as close together as possible (Fig. 7). The root becomes ganglionated at once, the cells first appearing dorsally at the root of the general cutaneous component of the ramus oticus and ventrally between the dorsal and ventral lateralis roots and laterally of the communis root and geniculate ganglion (Fig. 2).

The cells of the Gasserian ganglion are mainly large, with many small ones among them, while those of the geniculate ganglion are all small, so that the general relations of the two ganglia can be determined in spite of their intimate fusion. Nevertheless the middle portions of the ganglia are so closely joined together that the actual boundary between them cannot be accurately fixed, though the general cutaneous component throughout clearly forms the dorso-lateral portion of the complex and the communis component the ventro-mesial and when the nerve trunks are made up peripherally the same relations prevail. Thus, the chief nerves derived from this complex are those of the infra-orbital trunk and these, excluding the r. buccalis, go out in two bundles which WRIGHT termed the "supero-lateral strand" and the "infero-medial strand," of which the former is apparently wholly derived from the trigeminus roots (sensory and motor) and the latter from the communis root of the facialis. On account of the fusion of the ganglia just referred to it is impossible to demonstrate with certainty that these strands are purely trigeminal and facial respectively and that there is no admixture of their fibers, though the appearances certainly favor this and the peripheral distribution confirms it. In any case the number of mixed fibers must be small and the strands may, in my opinion, be regarded as practically pure as they leave the ganglionic complex, though WRIGHT's dissections led him to regard them as more or less mixed (84 a, p. 358.)

The whole of the trigemino-facial ganglionic complex is intra-cranial. The general cutaneous fibers for the periphery arising from the Gasserian ganglion leave the complex through four foramina: (1) dorsal general cutaneous fibers accompanying the r. oticus, arising from the most dorsal and proximal portion of the ganglion. (2) A small number of fibers arising near the last pass down external to the dorsal lateralis root and to the rest of the Gasserian ganglion, where they are reenforced by others from the ventral edge of the Gasserian ganglion just dorsally of the ventral lateralis root (see Fig. 2). Both groups, together with a small bundle from the geniculate ganglion, join the ventral lateralis root, all going out by a common foramen and forming the hyomandibular trunk. (3) By far the larger number of general cutaneous fibers enter the "supero-lateral strand," leaving the cranium by a common foramen with the "infero-medial strand" to enter the maxillary and mandibular branches of the trigeminus. (4) The remainder continue cephalad within the cranium, finally to enter the r. ophthalmicus superficialis trigemini.

### 3. *The communis root.*

This root does not enter the fasciculus communis, as in most other teleosts, to terminate with the IX and X nerves in the lobus vagi; but a special terminal nucleus is developed for it, the lobus facialis, or "lobus trigemini" of the older authors. Of course, the latter term is inadmissible now that we recognize this as a facial root. The morphology of this root and its cranial nucleus have been clearly presented by KINGSBURY ('97). It leaves the brain closely wedged in between the common lateralis root above and the large motor facialis below. The former of these roots at once divides, its ventral division passing down the outer side of the communis root. A little farther cephalad the trigeminus root emerges and bounds the inner side of the communis root, the dorsal lateralis root, the ventral lateralis root and the motor facialis lying external to it (Fig. 8). The communis root becomes ganglionated first on its lower border, then on the inner side, a group of cells continu-

ous with the latter running up just cephalad of the emerging trigeminus root and enlarging above the latter to form the ganglion of the r. lateralis accessorius (Figs. 2 and 7). A few communis fibers separate from these cells to go out with the r. oticus. The main cellular mass of this communis or geniculate ganglion lies ventral and internal to the other members of the complex, as described in connection with the Gasserian ganglion. A small bundle of fibers leaves the ventral edge of the ganglion for the truncus hyomandibularis and a short distance cephalad the r. palatinus posterior separates, leaving the cranium by the same foramen as the infra-orbital trunk. The palatine nerve separates from this trunk considerably farther cephalad outside of the foramen. All of the other communis fibers enter either the r. ophthalmicus superficialis trigemini or the "infero-medial strand" for the maxillary and mandibular branches of the trigeminus.

#### 4. *The lateralis roots.*

The dorsal and ventral lateralis roots arise together, but, as mentioned above, immediately separate. The dorsal one with its ganglion retains its position as the most dorsal member of the complex and divides to form r. ophthalmicus superficialis facialis and the r. buccalis in the typical way. Similarly the ventral root and its ganglion run down the lateral face of the complex to enter the hyomandibular trunk. The first and last rami mentioned leave the cranium by their own foramina, the r. buccalis with the infra-orbital trunk. The further description and critique of the relations of the terminal nuclei of these sensory roots will be deferred for fuller treatment at a later time.

#### 5. *Comparative review of roots.*

In comparing the trigemino-facial roots of *Ameiurus* with those of *Silurus*, the description of STANNIUS ('49 p. 25) shows that the relations are substantially identical. His first root contains the general cutaneous and motor V, the second and third are the dorsal and ventral lateralis roots, the fourth is the communis and the fifth the motor VII. The descriptions given by

JUGE ('99) in his recent monograph on the nerves and muscles of *Silurus* are more difficult of correlation. His work was done by dissection and macération in 10% nitric acid, without microscopic control, a method obviously inadequate to unravel completely so intricate a ganglionic plexus. But he labored under the further disadvantage of following in his morphological interpretations the erroneous scheme of GORONOWITSCH. I have previously commented at length ('99, p. 290-291, 366-399) upon the defects in this author's tri-metameric analysis of the trigemino-facial complex of the fishes in which he finds three segmental nerves, each with dorsal sensory and ventral motor root, in this complex. His first unit is the first root of STANNIUS, as I have enumerated them above, the second unit is the dorsal and ventral lateralis roots, the latter erroneously regarded as motor, and the third unit is the communis and motor facialis roots. Now JUGE not only fails to recognize the impossibility of this scheme, but apparently wrongly identifies some of GORONOWITSCH's roots in *Silurus*. Pending a microscopic examination of this complex in *Silurus*, it will hardly be profitable to review all of JUGE's conclusions, though it is obvious that *Silurus* is much more like *Ameiurus* than his descriptions would imply. For instance, in his analysis on p. 67, his "deuxième portion" (line 2) is evidently the infero-medial strand of WRIGHT and hence composed of communis fibers, while the "troisième portion" is the supero-lateral strand of general cutaneous fibers. It follows, then, that the "deuxième portion" cannot be, as he states in the next paragraph, the same as the Trigemini I of GORONOWITSCH, for the latter is derived from the trigeminus or general cutaneous root.

We now pass to the detailed description of such of the branches of the cranial nerves of *Ameiurus* as are german to the present point of view. The motor rami will not be fully described as I have merely confirmed the description of earlier students of the siluroid fishes in most of these cases. The innervation of the pharyngo-clavicularis, trapezius and a few other muscles, regarding which authorities differ, will be considered more at length, however.



6. *Ramus oticus.*

This nerve arises from the dorsal part of the ganglionic complex just cephalad of the origin of the r. lateralis accessorius and carries lateralis, general cutaneous and communis fibers (Figs. 1, 2). The lateralis fibers arise separately from the others, join them for only a very short distance, and separate at once, running back in the bony lateral line canal of the post-frontal and squamosal bones internal to the membranous canal to supply the first organ of the main canal, which lies in the squamosal bone. The general cutaneous and communis fibers run through the cranial roof laterally of the main canal and supply the adjacent skin and that of the dorsal part of the operculum. This whole region is plentifully supplied with terminal buds and small pit organs, probably supplied by communis and lateralis fibers respectively which accompany the general cutaneous fibers last mentioned, though their innervation was not demonstrated. These general cutaneous fibers occur also in *Clarias* (POLLARD, '92) and probably correspond to some (but not all) of the similar nerves described by STRONG ('95) for the tadpole of the frog as accessory trigeminal branches. (On the homologies of these latter nerves in the *Amphibia*, cf. COGHILL, '01).

Another slender nerve belonging to the lateralis system arises immediately caudad of the r. oticus from the dorsal lateralis ganglion (Figs. 1, 2, 6, 7, *n. 5* and *n. a. l.*), which may conveniently be described here, though it doubtless belongs morphologically with the r. ophthalmicus superficialis VII. This nerve runs up along the lateral aspect of the optic lobes and soon divides, one portion directed cephalad and one caudad, both running for a considerable distance intra-cranially. The former portion runs under the cranial roof to the level of the fifth organ of the supra-orbital canal and here (Fig. 6, *n. 5*) pierces the cranium to supply this organ. The portion directed caudad (Figs. 1, 2, *n. a. l.*) was traced into one of a series of three naked neuromasts in a row extending caudad from the last pore of the supra-orbital canal (Fig. 1, *al.*) and evidently

corresponding to the "anterior pit line" of *Amia* (ALLIS, '89). The other two organs are doubtless innervated from this same twig. This nerve clearly represents the nerve for the seventh supra-orbital lateral line organ and for the anterior pit line in *Amia* and the nerve for the seventh organ of the supra-orbital canal of *Batrachus* (CLAPP, '99). From the brief mention of STANNIUS ('49, p. 48) it is evident that *Silurus* presents a fiber complex in connection with the r. oticus similar to that described in this paragraph.

7. *The hyomandibular trunk.*

This trunk receives four components, viz. the motor VII root, the ventral lateralis root of the facialis, and small general cutaneous and communis strands. The mode of origin of the two latter from their ganglia has already been described. The lateralis root forms the r. mandibularis externus VII. The motor facialis root in part enters the r. hyoideus, where its fibers supply the branchiostegal muscles in the typical way, and the remainder of this motor root distributes with the branches which I included in the account of *Menidia* under the term r. opercularis profundus facialis. These branches supply the following muscles: adductor arcus palatini, adductor hyomandibularis, levator operculi, adductor operculi. The arrangement of these nerves in *Ameiurus* conforms to that of teleosts in general, save that, as is well known, the twig for the m. adductor arcus palatini supplies a separate slip of that muscle which serves as the abductor of the maxillary barblet. The general cutaneous fibers of the hyomandibular trunk here, as in teleosts generally, are to be regarded as secondary accessions to the facialis segment from the trigeminus. The communis fibers in the hyomandibular trunk apparently do not, as in the tadpole of the frog and *Menidia*, form a r. mandibularis internus VII, since this nerve is, as in *Gadus*, totally wanting. For no fibers from the hyomandibular trunk could be traced to the mucous lining of the mouth, either to terminate with free endings or to supply taste buds. On the other hand, all communis fibers of the truncus hyomandibularis seem to terminate in terminal buds

of the outer skin, chiefly in the region of the lower end of the preopercular bone.

The motor branches belonging to the deep opercular nerves are given off from the truncus immediately distal to the foramen of exit and then no other branches are given off until the trunk divides into the r. hyoideus and the r. mandibularis externus VII. The nerves corresponding to the r. opercularis superficialis VII of many other fishes seem not to be represented in *Ameiurus*.

8. *Ramus hyoideus.*

This nerve separates from the external mandibular at the outer edge of the hyomandibular bone and apparently receives from the trunk motor and general cutaneous fibers only. It descends at once into the branchiostegal apparatus, whose skin and muscles are innervated by it. The skin of the outer surface of the branchiostegal membrane bears occasional terminal buds and small pit organs which may be supplied from this nerve, though their fibers could not be traced.

The more fleshy inferior part of the m. hyohyoideus lies close under the m. geniohyoideus and between these muscles some filaments of the r. hyoideus effect minute terminal anastomoses with the motor trigeminal fibers for the latter muscle, similar to what ALLIS described for *Amia* ('97, p. 613) and I have described for *Gadus* ('00, p. 278). The sections leave no room for doubt, however, that no appreciable portion of the geniohyoideus is supplied from the facialis and WRIGHT is evidently in error when he gives the innervation of this muscle and of the intermandibularis from the facialis ('84 a, p. 369). The innervation of these muscles in *Silurus* is given by JUGE ('99, p. 28, 29, 32) as I have here described.

9. *Ramus mandibularis externus facialis.*

After separating from the r. hyoideus this nerve carries both coarse and fine fibers. The former comprise all of the lateralis fibers of the hyomandibular trunk, the latter are general cutaneous and communis fibers so intimately mingled that it is not possible to distinguish them until they separate for

their respective termini in the skin. Upon emergence from its canal in the preopercular bone the hyomandibular trunk divides at once into the r. hyoideus and the r. mandibularis externus and the latter nerve turns at once by a right angle and runs cephalad along the outer face of the hyomandibular bone, from which, however, it is separated by a wing of the preoperculum. In this position, internal to the ventral edge of the m. adductor mandibulae, the nerve divides into two branches: the smaller one is external running cephalad close under the skin and may be termed the cutaneous branch of the r. mandibularis externus VII (*cut. m. ex. VII*, on Fig. 1), while the larger branch enters the alveolar canal and supplies the organs of the mandibular canal in the way typical for the main r. mandib. ext. of other teleosts (*r. man. ext. VII*, of Fig. 1). The latter branch apparently carries only lateral line fibers, while the former includes communis, and probably also general cutaneous fibers, as shown by their peripheral distribution.

Before the separation of these two branches a lateral twig leaves the nerve for the last (eighth) organ of the operculo-mandibular canal and two or three smaller twigs for the skin adjacent, some of whose fibers were definitely traced into terminal buds. They doubtless also contain general cutaneous fibers for the same area, viz. the region of the caudal part of the preopercular bone. The few general cutaneous and communis fibers of the external mandibular nerve not thus distributed go out for the most part with the earlier twigs of the cutaneous branch for the skin under and behind the eye. Some of these were definitely traced to terminal buds. The source of the nerve supply of the small pit organs of the same region was not determined, probably from these same twigs.

The main external mandibular nerve, after supplying the seventh organ of the operculo-mandibular canal, passes down through a notch between the preoperculum and the hyomandibulare to the ventral side of these bones then, after a second ventrally directed bend, runs cephalad under the interoperculum and external to the quadrate. Upon entering the mandible this nerve takes up the usual position along the inner face of the

articular bone and farther cephalad between the dentary bone and MECKEL'S cartilage. In the latter position it crosses internal to the r. mandibularis V, with which however it does not anastomose, and then enters the bony lateral line canal in the dentary bone, innervating there its first and second canal organs. The organs of the operculo-mandibular canal are innervated by successive branches of this nerve as shown on Fig. 1, and no branches were traced to pit organs or any other distribution.

The cutaneous branch, on the other hand, supplies no canal organs. Its chief distribution is to small pit organs, large pit organs and terminal buds of the skin dorsal and external to the operculo-mandibular canal, though, as we have seen, the proximal portion carries general cutaneous fibers also for the outer skin adjacent to the canal behind the eye. This nerve runs cephalad near the skin under the ventral edge of the m. adductor mandibulae, then under the skin of the lateral face of the mandible, slightly dorsally of the course of the main r. mandibularis internus VII. It gives off numerous small branchlets for the small pit organs freely distributed along its course and also for a number of large pit organs which are scattered along the course of the canal, as shown in Fig. 1. The most caudal half dozen of these large pit organs are arranged in an irregular line running obliquely caudad and dorsad above the opercular canal and correspond to the cheek line of pit organs shown in Fig. 14. The cutaneous branch apparently carries general cutaneous fibers no farther cephalad than the eye, and in the mandible it follows closely the ventral side of a large cutaneous twig of the r. mandibularis V, from which the general cutaneous nerve supply of this region is derived. Common fibers, on the other hand, appear to accompany this nerve to its ultimate ramifications, and terminal twigs from most of its branches were definitely traced into both small pit organs and terminal buds.

COLLIDGE ('95, p. 281) makes the surprising statement that the mandibular canal of *A. catus* is supplied by the external ramus of the r. mandibularis V. This is certainly not true for *Ameiurus* and probably not for any other fish. Regarding

the facial group (by which he means the hyomandibular nerve, the other facialis branches being relegated by this author to the trigeminus) he adds: "No portion of the facial nerve, so far as I have been able to trace, innervates any portion of the sensory canal system. As previously pointed out, the descending branch of the ramus oticus replaces the hyomandibular branch of the facial in the upper portion of the operculo-mandibular canal, while the lower portion is innervated by the ramus mandibularis of the trigeminal, the mandibularis of the facial lying below it." The arrangements of the cranial nerves of *A. catus* are unquestionably similar in all essentials to those of *A. melas*. Further comment on the brief descriptions of this author will hardly be necessary.

So far as observed no fibers from the truncus hyomandibularis reach the mucous lining of the mouth. In *Ameiurus*, therefore, as in *Gadus*, there is no nerve corresponding to the r. mandibularis internus VII, as in the tadpole of the frog (STRONG, '95), in *Amia* (ALLIS, '97), in *Menidia* (HERRICK, '99), in *Lota* (GORONOWITSCH, '96), in some selachians (STANIUS, '49 and GREEN, 1900) and in many other fishes.

#### 10. *Ramus palatinus posterior.*

The nerve which in *Menidia* and *Gadus* I designated as the r. *pre-trematicus facialis* can be clearly identified in *Ameiurus*, though in a somewhat atypical form. This is the nerve named by WRIGHT ('84 a, p. 367) the r. cutaneus palatinus (a most unfortunate term), and I confirm his description of its course. JUGE ('99, p. 69) describes it for *Silurus* under the name, "rameau de la muqueuse buccale." My reason for returning to the term, r. *palatinus posterior*, which is devoid of morphological implications, will appear below.

It has an independent origin from the ventral edge of the geniculate ganglion (Figs. 2 and 6, r. *pt.* VII) and closely associated with the origin of the communis fibers for the hyomandibular trunk. It leaves the cranium immediately cephalad of the hyomandibular trunk and runs down at once to the submucosa of the roof of the mouth where it breaks up into numer-

ous branches for the adjacent parts of the wide palate and its taste buds, some branches running out into the mucous lining of the suspensorium (hyomandibulare, cartilaginous symplectic and quadrate) and of the proximal part of the hyoid arch. This whole region is freely supplied with taste buds which are innervated from these nerves. The middle and ventral parts of the hyoid arch are also supplied with taste buds, but they are innervated from a different source; viz. by a twig of the lingual branch of the post-trematic branch of the glossopharyngeus, which turns caudad from the point of union of the hyoid arch with the copula and follows the dorsal surface of the ceratohyal back as far as the region supplied by the nerve now under consideration. The lining of the mandible is freely supplied with taste buds, especially toward the distal end of the ramus. But none of these are supplied from the facialis, but from a branch of the r. mandibularis V which early becomes detached from that nerve and finally terminates in the lower breathing valve.

The posterior palatine branch of the facialis in *Ameiurus* as compared with the corresponding nerve of other fishes presents two features which are apparently abnormal; viz. (1) its origin is far removed from that of the r. palatinus, and (2) it runs down caudad of the pseudobranch, instead of cephalad of that organ. Its position is, however, really perfectly typical, the other two organs having been displaced cephalad. The r. palatinus arises from the infra-orbital trunk much farther cephalad than in teleosts in general, and this can only be regarded as a secondary modification. The pseudobranch (first described by MCKENZIE, '84, p. 426, whose description I confirm) is in a very rudimentary condition, a mere rete mirabile on the internal carotid artery (Fig. 3, *psbr.*). That it has suffered very great secondary displacement cephalad is obvious, its anterior extremity actually lying under the foramen by which the optic nerve leaves the cranium. The r. palatinus runs along its outer face and if it receives any cerebro-spinal nerve supply (which I consider improbable), it would doubtless be from this latter nerve.

The abnormal position of the nerve which I here term the

posterior palatine with reference to the pseudobranch does not therefore necessarily militate against the belief expressed in my earlier papers that this nerve is homologous with one of the pre-trematic branches of a typical branchiomic nerve. But it can hardly be regarded as the true pre-trematic ramus in the strict sense, i. e., the nerve for the mandibular demibranch (cf. GREEN, 1900), as I have regarded it in the case of both *Menidia* and *Gadus*, for here it has nothing to do with the pseudobranch or any other structure which might be associated with a rudimentary gill. It bears a closer resemblance to the nerve in selachians which Mr. GREEN and I have compared with the chorda tympani. Indeed this resemblance is strikingly close, though it may be impossible to decide whether it is an actual survival of that condition or whether we have here a nerve primitively connected with a spiracular demibranch which upon being emancipated from its gill secondarily extended into the hyoid arch.

The provisional identification of this nerve in *Menidia* as the r. pre-trematicus facialis was based primarily on its relation to the pseudobranch, and the morphology of the teleostean pseudobranch is at present in a most unsatisfactory state, as I pointed out in a brief survey of the literature in the *Menidia* paper ('99, pp. 329-332). This organ was tentatively regarded as a vestigial mandibular demibranch largely on the basis of MAURER'S ('88) embryological studies of the arterial arches of the salmon. The matter cannot, however, be regarded as definitely decided, for it appears from some researches by Mr. F. J. COLE now in process of publication that in *Pleuronectes* the vascular data indicate that the pseudobranch is hyoidean. I am permitted to quote from private correspondence from Mr. COLE, as follows: "As to the pseudobranch, in the plaice the nerve corresponding to JACOBSON'S anastomosis of the cod is a very large nerve, whilst the so-called pre-trematic VII is small. Both join and go to the pseudobranch." "Your pre-trematic VII = communis IX + communis VII [in the cod and plaice, but not in *Menidia* and *Ameiurus*, since these latter forms lack the JACOBSON'S anastomosis—C. J. H.]. Therefore



the pseudobranch of the cod may be supplied either by the communis IX or communis VII or both. Further than this only degeneration experiments will show. In the plaice we learn from the blood vessels that the pseudobranch *is a hyoidean demibranch* but nothing more. Further, that it is supplied by the IX nerve (mostly) and also perhaps by VII *is absolutely certain*. Let us suppose, therefore, that the pseudobranch of the plaice and cod is a posterior demibranch on the hyoid arch. Then JACOBSON'S anastomosis (there being otherwise no pre-trematic IX in the plaice) is the pre-trematic IX (+ palatinus also?), and your pre-trematic VII is the post-trematic VII. Further, when STANNIUS and PARKER refer to the IX supplying the pseudobranch, *they are referring to JACOBSON'S anastomosis*, and surely they are also right." Of course, if the teleostean pseudobranch proves to be, as here suggested, a hyoidean demibranch, rather than mandibular, then the posterior palatine must be the post-trematic branch of the facialis, if it is a branchial nerve at all. It will accordingly, be safer to avoid the term r. pre-trematicus VII in this connection until the morphology of the pseudobranch is more definitely known in a larger series of teleosts. Mr. COLE in this same correspondence calls attention to an error in my memoir on the cod fish ('00, p. 287), where it is stated that JACOBSON'S anastomosis runs from the facialis to the glossopharyngeus. Of course it is to be expected theoretically that these fibers would take the opposite course, if these commissural fibers represent (as I believe they do) the palatine branch of the glossopharyngeus. Renewed examination of my sections of *Gadus* indicate that his criticism is sound in fact, as well as in theory, for the evidence is that these fibers do arise from the IX ganglion and run forward. I was misled by the fact that the apparent size of the commissural nerve diminishes rapidly as it passes caudad from the junction with the facialis. In *Ameiurus* there is no JACOBSON'S anastomosis, though the palatine branch of the glossopharyngeus is very large and extends cephalad in the roof of the mouth near the median line nearly as far as the level of the foramen of exit of the posterior palatine. The latter nerve,

however, is directed outward and forward to reach the sides of the wide pharynx and hence the glossopharyngeal nerve does not reach it to effect the typical anastomosis.

#### 11. *Ramus palatinus.*

As intimated above, this nerve does not in *Ameiurus* arise from the ganglionic complex in its customary position between the hyomandibular and infra-orbital trunks, but in connection with the latter some distance farther cephalad. It separates from the "infero-medial strand" extra-cranially before that communis bundle has been distributed into the maxillary and mandibular nerves (Fig. 4, *r. pal.*). It then runs cephalad internally of the *r. maxillaris* and between it and the pseudo-branch (Fig. 3) and dorsally of the *m. adductor arcus palatini*. It supplies the mucosa of the roof of the mouth and its taste buds cephalad of the region supplied by the posterior palatine nerve and including the premaxillary teeth, as described by WRIGHT ('84 a, p. 367).

#### 12. *The infra-orbital trunk.*

This complex receives the ventral lateralis root for the *r. buccalis*, the motor trigeminus and the general cutaneous roots for the supero-lateral strand, and the communis root for the infero-medial strand. The latter gives off the *r. palatinus*, as just described, and then combines with the supero-lateral strand to form the maxillary and mandibular rami, the latter receiving all of the motor fibers and each nerve receiving both types of sensory nerve fibers in approximately equal proportions. The mandibular ramus will first be described.

#### 13. *Ramus mandibularis trigemini.*

The motor component of the supero-lateral strand lies laterally of the general cutaneous component and before this strand loses its individuality a bundle leaves the motor component (Fig. 5, *r. l. a. p.*) for the *m. dilator operculi* and the *m. levator arcus palatini*. Another and larger motor nerve follows soon (Fig. 4, *r. ad. man.*), running out over the origin of the slip of the *m. adductor mandibulae* which functions as the ad-

ductor of the maxillary barblet, and supplying this slip and the m. adductor mandibulae.

The mandibular nerve as soon as formed turns laterally over the m. adductor tentaculi, just referred to, close under the eye then ventrally into the lower jaw, previously, however, sending a twig out laterally for the skin under the eye and another cephalad which follows the dorsal surface of the m. retractor tentaculi and its tendon and finally enters the maxillary barblet behind (caudad of) the nerves for this barblet which come from the r. maxillaris. This posterior nerve of the barblet carries both general cutaneous and communis fibers. Before entering into the mandible the r. mandibularis divides into two branches, the smaller one running down external to the bones of the mandible, the larger one internal to them.

The external branch runs cephalad along the outer face of the mandible for its entire length, supplying the overlying skin and its terminal buds (the pit organs of this region it will be remembered are innervated by a similar twig, the cutaneous branch of the r. mandibularis externus VII) and the edge of the lower lip. It emits close to its origin a twig which pursues a rather peculiar course. It runs down external to the insertion into the mandible of the m. adductor mandibulae and then turns caudad along the dorsal surface of the mandible under the insertion of this muscle. Some of its fibers cross the cutaneous branch of the r. mandibularis externus VII, passing internally of it, for the skin over the dentary and angular bones. Others turn inward toward the buccal mucosa, which however they do not reach, but seem to break up over the articular and quadrate bones, probably for the overlying skin.

The internal branch follows along the dorsal side of MECKEL's cartilage (the r. mandibularis externus VII lying ventrally of this cartilage) and farther forward enters the alveolar canal, giving off for its entire length filaments for the mucous lining of the mandible and for its teeth. Within the alveolar canal it descends between the dentary bone and MECKEL's cartilage and divides into several branchlets. One of these carries all of the remaining motor fibers and turns inward to supply

the geniohyoid and intermandibular muscles. Both of these muscles are said by WRIGHT ('84 a) to be innervated by the facialis in *A. catus*; but there is really no opportunity for confusion in my specimens, as is the case with so many teleosts, since this motor nerve does not at any point come into relation with the facialis. Two other branches supply the mental and post-mental barblets respectively and the remainder of the nerve supplies the middle of the lower lip, the lower breathing valve and the teeth, all of these regions being plentifully supplied with taste buds. The barblets are supplied by fine fibers (chiefly communis, without doubt), as STANNIUS mentions ('49, p. 46) in the case of *Silurus*. The r. mandibularis V most emphatically does not supply the mandibular lateral line canal, as COLLINGE states ('95, p. 281).

#### 4. *Ramus maxillaris.*

The way in which this nerve receives its communis and general cutaneous components has already been described. But proximally of this level, while the supero-lateral and infero-medial strands are still distinct, a slender bundle is given off from each of them. These unite to form a nerve comparable with the accessory maxillary nerves of STRONG's description of the tadpole of the frog. (Figs. 2, 3, 4, 5, *ac. mx.*) It runs out laterally over all of the other members of the infra-orbital complex, laterally of the oculomotorius, mesially of the buccal, but at a slightly more dorsal level than either of these, and follows closely the course of the outer buccal branch, with which it finally fuses intimately. The fibers of both nerves are distributed in many branchlets to the skin behind, under and above the eye, the lateralis fibers to small pit organs, the communis fibers to the terminal buds which are very abundant at the edges of the eye, and the others to the skin in general. Some probably run out on to the cornea, though this was not actually observed. This nerve very clearly corresponds with the general cutaneous fibers distributed with the outer buccal branch of *Gadus* and probably with those from the r. ophthalmicus superficialis V accompanying the twig marked *cil.* on

Plate XXI of my *Gadus* paper ('00). In *Ameiurus* the three components are so intimately united in this nerve that even small terminal branchlets often contain all of them, as shown by the fact their fibers may supply the skin in general, terminal buds and pit organs.

The r. maxillaris runs parallel with the r. mandibularis until that nerve under the eye turns laterally toward the mandible. In this region it divides into two unequal branches, the larger becoming lateral, the smaller mesial. The latter runs forward between the palate bone and the m. adductor tentaculi and its tendon and then divides into four branches of which three enter the maxillary barblet along with the twig from the r. mandibularis, already described, while the fourth distributes to the skin of the upper lip just cephalad of the insertion of this barblet. The mesial branch runs over the palatal bone and under the nasal sac, closely accompanied by the terminal twig of the r. buccalis for the premaxillary pit line across the tip of the snout, and distributes to the lateral premaxillary teeth and the skin and taste buds of the lateral parts of the upper lip, as described by WRIGHT.

JUGE ('99, p. 73) finds in *Silurus* a branch of the r. maxillaris which temporarily fuses with the r. ophthalmicus superficialis V (his oph. profundus) and separates to supply the alveolar region of the pre-maxillary bone. A twig from this nerve anastomoses with the r. palatinus VII. It is instructive to compare this anastomosis with similar ones between the ophthalmicus profundus and the palatine in the *Amphibia* (cf. COGHILL, '01).

#### 15. *Ramus buccalis.*

This third member of the infra-orbital complex is, as usual among the teleosts, quite intimately joined with the r. maxillaris, from which, however, WRIGHT was able to separate it peripherally as well as centrally. But his statement ('94 a, p. 367) that "it contains fibers other than those derived from the tuberculum acusticum" does not apply to the species of *Ameiurus* which we are now considering, for at no point in its course

save at the peripheral ends of some of the minor branches does it receive other than lateralis fibers. Cf. Figs. 1, 2, 3, 4, 5, *r. buc.*

As soon as the maxillary and mandibular nerves are formed the *r. buccalis* takes up a position dorsally of them and in the notch between them, at the same time sending off a considerable branch laterally which is comparable with the outer buccal branch of *Gadus*. (Figs. 1, 2, 3, 4, *out. buc.*) This branch runs outward in the narrow space under the *m. levator arcus palatini* and above the *m. adductor tentaculi* closely accompanied by the accessory maxillary nerve (*ac. mx*). Having reached nearly to the caudal border of the eye, the two nerves anastomose and break up into numerous branchlets. One lateralis twig supplies the sixth organ of the infra-orbital canal, two others run back under the sixth sub-orbital bone and apparently supply small pit organs behind this region, while another runs farther laterally to supply small pit organs near the fifth infra-orbital canal organ and a line of similar organs extending caudad from this point continuing in the direction of the horizontal limb of the infra-orbital canal. The later twig is comparable with the one marked *b. p. o.* on my plot of *Gadus* ('oo, Plate XXI).

A small twig arises just in front of the outer buccal and may be regarded as a detached filament of that nerve, running along the lateral side of the mandibular nerve for a short distance, then turning out under the eye, to innervate the fifth sense organ of the infra-orbital canal (*r. s. 5*; Figs. 1, 3). At the point where the *r. mandibularis* separates from the infra-orbital complex to enter the lower jaw the *r. buccalis* divides into three branches. The smaller one runs out under the eye to supply the fourth organ of the infra-orbital canal. One of the other branches supplies the third organ of this canal and small pit organs along the entire length of the horizontal limb of the infra-orbital canal, and also sends a twig forward to anastomose with the nerve for the second organ. The third branch sends a twig to the second canal organ, which first receives the anastomosing twig just referred to, then a branch for the first organ, which also sends

a minute twig to the skin adjacent, presumably for the small pit organs over the lachrymal bone. The remainder of the buccal nerve runs forward under the nasal sac to distribute to a row of five or six large pit organs near the anterior nasal aperture and doubtless to small pit organs also in the same vicinity, though the latter point was not actually observed. Together these larger organs form a row corresponding to the "maxillary commissure," or organs *b, c, d, e, f*, of *Menidia* and to the lines of naked organs in the corresponding position of *Lophius* (GUITEL, '91), *Batrachus* (CLAPP, '99), and *Gadus* (COLE, '98, p. 158 and HERRICK, '00 p. 281). ALLIS has previously mentioned this line ('97, p. 629). STANNIUS ('49, pp. 41, 43) and JUGE ('99) affirm that the r. buccalis is absent in *Silurus*, which of course can only be interpreted to mean that it is not anatomically distinct. The latter author mentions in his summary (p. 159) that the suborbital lateral line canal is innervated by a twig from the inferior branch of the r. ophthalmicus superficialis facialis (JUGE relegates this nerve, however, to the trigeminus and calls the true r. ophthalmicus superficialis V the ophthalmicus profundus). Unfortunately he does not give, so far as I can find, a more exact description of this nerve. If the fact is as stated, it simply means that in *Silurus* the dorsal and ventral branches of the dorsal lateralis root of the facialis separate into r. ophthalmicus superficialis VII and r. buccalis far distal to their common foramen instead of intra-cranially as in teleosts generally.

16. *Ramus ophthalmicus superficialis facialis.*

This nerve has been examined and briefly reported upon by my pupil, MR. WORKMAN ('00, p. 403), his studies having been based upon the same sections as those now under consideration. Its fibers separate from the dorsal side of the ganglionic complex (see Fig. 2) and are purely lateralis fibers with no admixture of other components. Emerging from the cranium by a separate foramen, it supplies all of the organs of the supra-orbital canal (except the fifth organ, supplied by the r. oticus) and small pit organs along the course of this canal. The general arrangement

of the branches is indicated on Fig. 1, all twigs not supplying canal organs being distributed to small pit organs.

17. *R. ophthalmicus superficialis trigemini.*

The three components which in most teleosts are bound up together to form the supra-orbital trunk (compare the account in the Menidia paper, '99) in the siluroid fishes are arranged in two distinct groups. One of these is the r. ophthalmicus superficialis VII, which has been described just above; the other is the so-called r. ophthalmicus superficialis V, containing in Ameiurus general cutaneous and communis fibers in about equal proportions. The course and morphological significance of this nerve have been discussed in detail by MR. WORKMAN ('00) and these details need not be repeated here. I will merely copy his summary of the course of this nerve.

"To recapitulate, the r. ophthalmicus superficialis trigemini arises from the ganglionic complex slightly cephalad and ventrad of the r. ophthalmicus superficialis facialis, emerges through the cranium by a separate foramen, and pursues an entirely separate course peripherally, lying ventrally of the latter nerve and widely separated from it by the fleshy origin of the m. dilator operculi. In front of the orbit it passes through a foramen in the frontal bone to run forward close to but distinct from the facial ophthalmic nerve. It distributes to the skin and its contained terminal buds in front of the eye, about the nasal apertures and in front of the latter and to the nasal barblet—about the same distribution, in short, as the fibers of the r. ophthalmicus superficialis facialis destined for pit organs contained in large numbers in this same area of skin. In no case were the fibers of the facial nerve observed to enter terminal buds nor those of the trigeminal nerve to enter pit organs. The trigeminal ophthalmic nerve undoubtedly innervates the skin in general of this area by means of its general cutaneous fibers and the terminal buds by its communis fibers, the large size of the communis component observed to enter the nerve proximally being correlated with the enormous number of buds innervated."

From this account it follows that this nerve of siluroids



should not be called the r. ophthalmicus profundus, as has been done by WRIGHT and some others; but that it corresponds in all essential respects with the nerve commonly named the r. ophthalmicus superficialis V by teleostean anatomists. This term is also inappropriate, as I have before pointed out; for in *Ameiurus* fully half of its fibers are derived from the geniculate ganglion and therefore belong to the facialis and not to the trigeminus. In *Amia* too ALLIS finds a large communis element in this nerve, with similar distribution, viz. for terminal buds of the skin of the top of the head. Although the general cutaneous or trigeminal element is no doubt largely in excess in teleosts in general, as I have found it to be in *Menidia* and *Gadus*, yet the communis element seems to be uniformly present, even in cases like those last mentioned where there is no considerable number of terminal buds on the top of the head.

18. *Ramus lateralis accessorius.*

This nerve arises from the most dorsal and proximal portion of the geniculate ganglion. A compact mass of cells runs up along the inner side of the trigeminus root and ganglion and of the dorsal lateralis root which swells out above these roots at the level of the superficial origin of the trigeminus root into a larger ganglionic mass (Figs. 2, 7). Fibers of the r. lateralis accessorius arise from all of these cells and the nerve runs caudad within the cranium for a short distance as a large round bundle pressed as closely as possible to the dorso-lateral border of the oblongata.

From the ganglion at the root of the r. lateralis accessorius a slender twig rises up to the dorso-lateral angle of the cranial cavity and there runs cephalad in company with a big blood vessel, finally to break up over the cerebellum and perforate the cranial roof by many apertures, innervating terminal buds of the overlying skin. This nerve I have termed the meningeal ramus of the r. lateralis accessorius (*m*, Figs. 2, 5, 6). STANNIUS mentions a similar twig in *Silurus* ('49, p. 48).

The accessory lateral line nerve runs back under the cranial roof nearly to the caudal limit of the medulla oblongata before

passing out through its foramen, which is long and traverses obliquely the supra-occipital bone. Just before entering this foramen a small twig is given off for terminal buds scattered over the supra-occipital region and several others follow while the nerve is within the foramen. Beyond the foramen the nerve continues to run caudad near the median line in the usual position between the dorsal and interspinous muscles.

At the level of the first spinal nerve a small branch runs down from the *r. lateralis accessorius* along the lateral face of the occipital bone to join the ventral ramus of the first spinal nerve (Fig. 1, *sp. 1*). A few sections farther caudad it is followed by a much larger branch which joins the ventral ramus of the second spinal nerve (Fig. 1, *sp. 2*). The sections leave no doubt that these are *communis* fibers from the accessory lateral nerve for the spinals and not spinal nerves for the accessory *lateralis*. This is plain at their origin dorsally from the accessory *lateralis* and also ventrally at the union with the spinals. In the case of the first nerve the anastomosing twig enters the ventral ramus some distance distally of the spinal ganglion and the *communis* fibers run out with that ramus and do not turn back into the spinal ganglion. In the case of the second nerve the *communis* fibers pass into the spinal ganglion, but can clearly be traced through the ganglion, without entering into relation with its cells, into the ventral ramus.

The *r. lateralis accessorius* during its course through the trunk sends filaments at more or less irregular intervals dorsally toward the skin. It also, behind the second spinal nerve, effects the typical anastomosis with the spinal ganglia via the *r. communicans*. In the typical cases the *r. communicans* passes from the spinal ganglion dorsad and slightly caudad and enters the *r. accessorius* bodily. It doubtless carries some general cutaneous fibers from the ganglion which later leave the *r. lateralis* with some of its twigs for the dorsal body surface. But these fibers can form but a small proportion of the anastomosing branch; for the sections clearly show fibers from the *r. lateralis accessorius* entering this nerve and passing directly through the spinal ganglion to enter the corresponding ventral ramus. These

no doubt supply the terminal buds scattered sparsely over the ventral surfaces of the whole body.

The r. accessorius continues caudad with no change of relations as far as traced (half way through the body) in our sections. In the neighborhood of the dorsal fin its branches are neither larger nor more numerous than elsewhere, nor does the fin bear terminal buds in greater abundance than elsewhere on the trunk.

The dorsal rami of the spinal nerves are of the sort typical for teleosts; viz., (1) a r. communicans, sensory, and (2) a r. spinosus, motor. Both of these run up in the intermuscular space between the dorsal and inter-spinous musculature and may anastomose with the r. lateralis accessorius. The r. spinosus supplies only muscles, while the r. communicans contains general cutaneous fibers from the spinal ganglion for the skin of the dorsum and communis fibers from the r. lateralis accessorius for terminal buds of the lateral and ventral surfaces of the body.

WRIGHT states ('84 a, p. 366) that the r. lateralis accessorius of *A. catus* (his r. lateralis trigemini) is "reinforced immediately after leaving the skull by the important dorsal branches of the first, second and third spinal nerves, and acts as a collector for slenderer branches from all of the other *rami dorsales*." JUGE ('99, p. 96) makes a similar statement for *Silurus*. I have shown in my contributions on *Menidia* and *Gadus* that the r. lateralis accessorius is in no sense a collector of dorsal branches of spinal nerves in these fishes, and the same proves to be the case in *Ameiurus* also.

Inasmuch as I have found it impossible to follow the separate components of the brachial plexus (in particular the general cutaneous and communis elements), I have not worked out the detailed anatomy of this plexus. It is evident that the relations in *Ameiurus melas* are not identical with those of *A. catus*, as described by WRIGHT. So far as I have noticed, the chief differences of importance concern the relations of the spinal nerves to the r. lateralis accessorius. As we have already seen, the latter nerve sends a contribution to the ventral ramus of each

spinal nerve. Those which enter the brachial plexus no doubt distribute to the terminal buds found sparsely scattered over the pectoral fin and other cutaneous areas supplied by these nerves. The whole body surface as far back as the middle of the dorsal fin has been examined microscopically and is seen to be supplied with scattered terminal buds, which are unquestionably innervated by communis fibers from the r. lateralis accessorius either directly, in the case of the dorsal surface of the body, or by the communis branches from this nerve going out by way of the ventral rami of the spinal nerves.

POLLARD ('92, p. 530) says that in *Clarias* the r. lateralis accessorius "supplies the mucous canal at the base of the dorsal fin." Like several other recent writers, I am wholly at a loss to know to what he can refer. There is nothing like a canal in this position in *Ameiurus* and if such a canal occurs in any other siluroid it is most improbable that it should be innervated from this nerve. In the same paper POLLARD describes an anastomosis between the r. lateralis accessorius of *Clarias*, *Callichthys*, *Chaetostomus* and *Auchenapsis* and the r. supratemporalis vagi. This vagal branch cannot well be the vagal root of the r. lateralis accessorius, such as is found in *Gadus* and some other teleosts, for this root is of communis nature, while POLLARD's account shows that his anastomosing nerve is really the r. supratemporalis vagi, i. e., a lateralis nerve, for it supplies the first canal organ of the main line caudad of the one supplied by the IX nerve. The vagal root of the r. lateralis accessorius is certainly quite lacking in *Ameiurus*.

In the description of *Silurus* by JUGE ('99) it is stated that the r. lateralis accessorius (nerve of WEBER) probably receives fibers from all of the sensory trigemino-facial roots. We have seen above that in *Ameiurus* this nerve is purely communis as in all other cases where its exact composition is known. JUGE worked only by gross methods and there can be but little doubt that a more exact analysis will show that in *Silurus* this nerve, or at least the portion which enters the trunk, is wholly composed of communis fibers. Of course this throws quite out of court the homology of the nerve of WEBER with dorsal rami of

spinal nerves which JUGE repeats (p. 97) after STANNIUS, for, as I have so often emphasized, a communis nerve cannot be homologized with a general cutaneous nerve.

## II. THE GLOSSOPHARYNGEUS NERVE.

As usual among the teleosts, the motor IX root runs out ventrally of the spinal V tract and quite far removed from it. The communis root runs out dorsally of the spinal V tract and as close to it as possible and in passing it may receive a small general cutaneous component from it, though I have not been able to demonstrate such a connection, nor is it mentioned by WRIGHT or KINGSBURY. The sensory root and the motor root join soon after their emergence from the oblongata and both run back together under the root of the r. lateralis vagi, from which some fibers are detached to join the IX roots. A short distance cephalad of the vagus foramen the IX nerve passes out of the cranium by a separate foramen, just within which there is a small ganglion, which belongs to the lateralis component. The fibers from this ganglion can be clearly followed peripherally and constitute a ramus supra-temporalis IX, belonging to the lateralis component. Upon emergence from the IX foramen, it does not turn cephalad with the remainder of the glossopharyngeus, but caudad, then dorsally along the ventral surface of the parotic process of the cranium into a canal in the squamosal bone, where it divides into two unequal branchlets. The larger one supplies the second sense organ of the lateral line canal of the trunk within that bone; but the smaller one leaves the canal, directed toward the median line along the inner face of the squamosal bone nearly to its mesial border. Here it passes outward through a minute foramen in the bone and divides to innervate the two large pit organs which make up the middle pit line (Fig 1, *m. l.*)

Within the squamosal bone the r. supratemporalis IX anastomoses with twigs from the r. cutaneus dorsalis vagi and the relations are here somewhat confused. I think, however, that this nerve contains lateralis fibers only and no others. It is comparable with the branches of the IX nerve for canal or-

gans in the siluroid fishes described by POLLARD ('92). In these cases also there are cutaneous branches not destined for canal organs; but he does not indicate their composition. Of course, in enumerating this branch with the glossopharyngeus we must not lose sight of the fact that this is for convenience of topographical description merely. It has no real morphological connection with that nerve, being a branch of the r. lateralis vagi.

The conditions above described were found also in a second specimen and may be regarded as typical for this species, though on the opposite side of the specimen plotted this lateralis twig separates from the IX root intra-cranially and passes out through the vagus foramen, the other relations being as above described.

The remainder of the glossopharyngeus runs forward outside the cranium to its ganglion in the usual way. The details of the peripheral relations have not been fully worked out. The post-trematic ramus is very large. I have not succeeded in demonstrating a pre-trematic ramus, nor does WRIGHT mention it in his account of *A. catus*, and both STANNIUS ('49, p. 76) and JUGE ('99, p. 103) deny its presence in *Silurus*. The palatine ramus is distinct and can be followed as far forward on the roof of the mouth as the level of the chief foramen of the V+VII nerve complex, where it supplies large taste buds of the palate. No JACOBSON'S anastomosis was discovered; compare the discussion of the r. palatinus posterior, above.

### III. THE VAGUS NERVE.

The vagus roots, motor, communis, lateralis and general cutaneous, are arranged in the typical way, the motor root arising in several distinct strands ventrally of the spinal V tract and the communis root passing out dorsally of this tract. The general cutaneous root is quite large and joins the communis root as the latter passes over the spinal V tract. The general cutaneous fibers derived from the vagus follow the spinal V tract for only a very short distance, soon turning inward to terminate in the substantia gelatinosa mesially of the tract.

Both the sensory and motor roots run down internal to the lateralis root directly to their common foramen. The peripheral rami of the vagus which distribute to the skin have been fully worked out, while those for the gills and other viscera have been studied less thoroughly.

*1. The motor rami of the vagus complex.*

The motor rami will not be fully described save in two cases where the accounts in the literature are contradictory.

*The internal and external pharyngo-clavicularis muscles* are innervated from the vagus substantially as I have found them in *Menidia* and *Gadus*. WRIGHT states that they are innervated from the first spinals in *Amia* ('85, p. 138) and *Ameiurus* ('84 a, p. 371). ALLIS has shown ('97, p. 697) that the former is incorrect and now it appears that the latter is also an error. Thus the difficulty which I have referred to in the discussion of these nerves in *Menidia* ('99, p. 266) disappears so far as this type is concerned, and the pharyngo-claviculares of *Ameiurus* are shown to be homologous with these muscles of the other bony fishes. JUGE ('99, p. 40) finds that these muscles are innervated from the inferior pharyngeal branch of the vagus in *Silurus*.

*The trapezius muscle* is said by WRIGHT ('84 a, p. 371) to be innervated in *Ameiurus catus* by the first spinal nerve, stating that its ventral branch "rests on the trapezius muscle which it innervates." This is clearly an error, for I have traced the nerve supplying this muscle back into the vagus ganglionic complex and through this complex into the motor vagus roots. The first spinal nerve and ganglion pass close to the caudal edge of the vagus ganglion, but the microscope shows that there is no nervous connection between them. Nor do any fibers leave the spinal nerve for the trapezius muscle. Mc MURRICH is, therefore, doubtless correct, when he says ('84, p. 331) that the trapezius of *Ameiurus* corresponds with that muscle of selachians. This also agrees with the conditions found in *Menidia*, but not with those of the cod, as I have shown ('00, p. 298), nor with the forms described by VETTER. JAQUET

('98, p, 223) describes this muscle in *Silurus glanis*, where its occurrence is much as in *Menidia*. He does not mention its innervation. JUGE ('99, p. 42) describes it for *Silurus* with a slightly different mode of origin under the name "*musculature céphalo-scapulaire*" (or better "*élevateur claviculaire*"), and states that it is innervated by "a branch arising from the pharyngo-intestinal trunk of the vagus."

2. *Ramus cutaneus dorsalis vagi.*

The ganglion of the general cutaneous root of the vagus (jugular ganglion) lies, as usual among the teleosts, within the vagus foramen. It is quite large and occupies the cephalic aspect of the root complex. The peripheral fibers arising in this ganglion enter, for the most part, the *r. cutaneus dorsalis vagi*, running out of the foramen in the most caudal and dorsal part of the root complex closely following the *lateralis* root. Turning sharply dorsally they cross the dorsal surface of the *r. intestinalis*, and receive a twig from the *lateralis* ganglion destined for the third organ of the main lateral line canal. After separating from the vagus complex this nerve runs up around the parotic process of the cranium and at its outer angle breaks up into numerous branchlets for the skin of the occipital region, one of which runs down into the operculum. This latter branch is the *r. opercularis vagi*, supplying the lining of the caudal part of the operculum. None of the fibers of the *r. cutaneus dorsalis vagi* were traced to terminal buds, pit organs or other special sense organs. Its composition is therefore typical as compared with other teleosts, viz., general cutaneous.

From the jugular ganglion a delicate nerve passes directly dorsal in the meninges around the oblongata. It reaches the dorsal surface of the brain at about the level of the exit from the cranial cavity of the *r. lateralis accessorius*, and farther mesially, and I at first thought that it was a slender vagal root of the latter nerve, as its origin is similar to that of this nerve in *Gadus*. This, however, appears not to be the case, for it not only arises from the general cutaneous instead of the *communis* ganglion, but in no case could it be traced into the *r.*



lateralis accessorius. In one series in which this twig is larger than in others I traced it up to the skin of the dorsum in the fontanel between the two projections directed cephalad from the dorso-median part of the supra-occipital bone. STANNUS states ('49, p. 85) that this nerve is absent in *Silurus*, but JUGE finds it present in this species ('99, p. 106).

### 3. *Ramus lateralis vagi.*

The lateralis root of the vagus after separating from the caudal end of the tuberculum acusticum, runs back in the usual way dorsal and external to the VIII roots and the other members of the IX+X complex, emerging from the cranium by the vagus foramen. The twig, described above, which is detached to form the r. supra-temporalis IX apparently corresponds to a part of the r. supra-temporalis vagi of *Menidia* (viz. the twig for the organ in the squamosal bone); but seems not to be represented in that nerve of *Gadus*, for in the latter case the supra-temporal ramus does not supply any organ in the squamosal bone.

From the ganglion of the r. lateralis vagi are given off three small nerves.

(1) The first joins the r. cutaneus dorsalis vagi (from which, however, it can be distinguished microscopically by the larger caliber of its fibers) and with that nerve curves up around the parotic process, at the caudo-lateral angle of which the two nerves separate. The coarser lateralis fibers all enter the supra-temporal bone and innervate the single organ of the main lateral line canal therein contained.

(2) The second nerve passes directly outward to supply the fourth organ of the main lateral line, contained in the post-temporal bone.

(3) The third nerve (Fig. 1, *d. l.*) also runs dorsally around the parotic process and penetrates between the fibers of the dorsal musculature which arise from this portion of the cranium. Having reached the edge of the bone it divides, its branches being directed toward the mid-dorsal line, some caudad, some cephalad of the point of division. This region is

very abundantly supplied with small pit organs, into some of which twigs from this nerve were traced. All of the other fibers of this nerve apparently have a similar distribution, save four branchlets, which enter each a single large pit organ. Three of these lie in a row running transversely to the body axis mesially of the post-temporal bone, and one near the mid-dorsal line farther caudad by about the thickness of one myotome. These apparently correspond to the dorsal pit line of *Amia*, *Batrachus*, *Gadus*, etc.

The *lateralis* branch of the *vagus* runs back from its ganglion quite deeply embedded in the dorsal musculature under the lateral line of the trunk. Behind the pectoral fin it sends a minute twig outward to supply a single large pit organ situated just above the fourth pore of the lateral line canal of the trunk. At about the same position the lateral line nerve divides into ventral and dorsal branches, the latter being slightly larger. From the dorsal branch (Fig. 1, *d. lat. X*) two small twigs leave at once, whose ultimate distribution could not be accurately determined, probably for small pit organs farther dorsally. Then from the dorsal branch is given off the twig for the sixth canal organ, contained in the second drain-pipe bone, and immediately another dorsally directed twig for one of two large pit organs near the mid-dorsal line in the same transverse plane as the sixth pore of the trunk canal. The innervation of the other large pit organ just mentioned could not definitely determined, but is probably from a twig of the *r. lateralis* given off just caudad of the one for the sixth canal organ.

Successive organs of the trunk canal are supplied by twigs from the dorsal lateral line nerve and other twigs are given off for small pit organs sparsely scattered over the body and for large pit organs in an irregular longitudinal row near the mid-dorsal line and at occasional intervals near the body canal, becoming less frequent caudad. The nerve was followed and the skin examined microscopically as far back as the middle of the dorsal fin. None of the large pit organs were found save near the main canal or at various distances between it and the mid-

dorsal line. Small pit organs are, however, more uniformly, though sparsely, distributed over the whole body surface, including the base of the dorsal fin.

The ventral branch of the lateral line nerve (Fig. 1, *v. lat. X*) turns at once laterally and ventrally, anastomosing with the ventral ramus of a spinal nerve, passing close to the lateral line canal and supplying its fifth organ. This is the only organ of the lateral line canal supplied by this nerve. Other fibers supply a dense cluster of small pit organs about the base of the pectoral fin. The branch then runs back close under the skin laterally of the ventral musculature and supplies small pit organs of the skin ventrally of the lateral line canal as far back as my sections run, or nearly to the pelvic fins. This branch corresponds to the superficial branch of the lateral nerve of JUGE's description of *Silurus* ('99, p. 131).

#### IV. THE SYMPATHETIC NERVOUS SYSTEM.

The sympathetic system has not been carefully studied and I can add but little to the brief note given by WRIGHT ('84 a, p. 372), as its fibers have very poorly developed medullary sheaths or none at all and my methods are not well adapted for them. The system as a whole, as in *Gadus*, deviates far from the peculiarly complex arrangement which is typical for teleosts, though it may evidently be derived from that arrangement.

The sympathetic ganglionated chain of the trunk runs close to the centra of the vertebrae and so far as examined (*viz.* in the most cephalic spinal segments) contains ganglion cells quite uniformly scattered through it. Under the caudal end of the basi-occipital the ganglion cells disappear, to be followed farther cephalad by a large ganglion. The chain meanwhile approaches the median line and at the level of the vagus foramen meets the chain of the opposite side in a large unpaired ganglion. This ganglion bifurcates cephalad and the chains of the two sides rapidly separate, becoming non-ganglionated, and continue cephalad, under the basi-occipital mesially of the X and IX ganglia and separated from them by a big vessel. The non-ganglionated sympathetic cord continues forward along the

outer wall of the cranium cephalad of the IX ganglion, maintaining the same relation to the IX nerve until that nerve enters the first gill. At that level a long narrow ganglion appears in the chain. This ganglion appears close behind the point of exit of the hyomandibular trunk from its foramen and it communicates with this nerve and with the r. palatinus posterior. Unlike most other vertebrates, the sympathetic ganglionated chain does not touch directly either the vagus or the glosso-pharyngeus nerves at any point.

The sympathetic chain enters the trigemino-facial ganglionic complex with the hyomandibular trunk, and I was not able to trace its entire course through the complex. Apparently it divides, some fibers running forward along the outer surface of the complex and some farther mesially, the former strand probably entering the infra-orbital trunk. The latter strand reappears at the level of the exit of the oculomotor nerve from its foramen as a detached non-ganglionated strand of non-medullated fibers which runs out closely joined to the III nerve. Just cephalad of the point where the nerve for the m. rectus superior separates from the III nerve there is a small sympathetic ganglion of only six to ten cells. After the branch for the m. rectus inferior has separated from the III nerve the sympathetic also separates from it and immediately presents another small ganglion lying just dorsally of the m. rectus inferior between it and the orbital vein. From this ganglion a clearly defined compact bundle of fibers runs out laterally under the vessel just mentioned and reaches the eye-ball slightly caudad of the point where the optic nerve enters it. This nerve is clearly the r. ciliaris brevis.

## PART II. THE CUTANEOUS SENSE ORGANS.

Under this head it is proposed to present a few observations upon the two systems of cutaneous sense organs so abundantly scattered over almost the entire body surface of American siluroids; viz. the organs of the lateralis and terminal bud systems. We have seen in the previous sections that these two systems are very distinct in their innervation, the former being

supplied by nerves of the acustico-lateralis system and the latter by nerves of the communis system in all cases where the innervation can be determined with accuracy; and now it remains to inquire regarding the structure and arrangements of the organs themselves.

#### I. ORGANS OF THE COMMUNIS SYSTEM.

Here, as in other teleosts, the terminal buds of the outer skin and the taste buds of the mouth are not only similar in their innervation (communis nerves in both cases) but they are essentially similar in structure.

Fig. 11 illustrates a typical terminal bud from the skin of the top of the head. The skin has the typical structure so accurately described by WRIGHT ('84, p. 251, seq.), and the sense bud is seen to consist of a simple epithelium of enormously elongated cells. They are, however, hardly long enough to reach all of the way through the thick epidermis; accordingly the dermis is raised under the organ into a papilla upon the apex of which the sensory epithelium rests. The nerve pierces the dermis under the center of the organ and is composed of larger fibers than those ordinarily found in the communis system, with very densely staining medullary sheaths. This peculiarity of the nerve fibers is the only important difference which I have been able to discover between the terminal buds of the outer skin and the taste buds of the pharyngeal cavity. In both cases, when it is possible to trace the nerves back to their origin with precision, they are found to arise from communis roots of the VII, IX or X cranial nerves. In both cases the organs are strictly superficial and usually the apex lies in a papilla slightly elevated above the surrounding surface of the epithelium.

#### II. ORGANS OF THE ACUSTICO-LATERALIS SYSTEM.

Besides the organs of the internal ear, which are not considered in this contribution, there are three types of sense organs belonging to the acustico-lateralis system in *Ameiurus*, all lying in the skin or immediately beneath it. Following the

usage of WRIGHT, these may all be termed neuromasts, a term used by him as equivalent to the *Nervenhügel* of MERKEL. These types of organs are, (1) the canal organs, or sensory organs within the true lateral line canals; (2) the small pit organs, or similar sensory organs sunken into separate pits which have no connection with the lateral line canals; (3) larger sensory organs lying in the epidermis and nearly flush with its surface. These I have termed large pit organs and their structure differs in some respects from that of the other two types of organs.

1. *The lateral line canals and their sense organs in Ameiurus melas.*

Although the lateralis system as a whole is unusually highly developed, the lateral line canals themselves are not so, but present a very simple arrangement conforming closely to the teleostean type schema. The pores are never dendritic, as in *Amia*, but are simple and for the most part bear the typical relations to the sense organs and the cranial bones. In short, the specialized features of the lateralis system are found in the pit organs, not in the canals or their organs. The canals will be described under the head of supra-orbital, infra-orbital, operculo-mandibular and main canals, the latter being defined as the canal running caudad into the trunk from the point of union of the supra-orbital and infra-orbital canals. The relations of these canals to each other, to their sense organs and their nerves, and to such of the cranial bones as contain them are indicated on Fig. 1, in which the sense organs of each canal are numbered consecutively from before with Arabic figures and the pores with Roman numerals. This figure also shows the positions of the large pit organs, but not of the small pit organs.

a. *The supra-orbital canal.* The supra-orbital canal lies entirely in the nasal and frontal bones. It opens at each end upon the surface by means of pores and contains five sense organs, all separated by simple dermal tubules and surface pores save the last two. The most cephalic terminal pore opens just internally to the anterior nasal aperture at the anterior end

of the nasal bone. This bone contains two sense organs separated by a pore, and in the space between the nasal and the frontal there is a third pore. In the frontal bone there is a pore between the third and fourth organs, and between the fourth and fifth organs this canal communicates with the infra-orbital. At this point there are four diverging canals; viz., the infra-orbital, directed ventrally, the main canal running back into the trunk, the supra-orbital, directed forward, and a short limb of the supra-orbital running backward and inward. This short canal opens by a pore at the caudal end of the frontal bone and contains a single sense organ, which I term the fifth supra-orbital organ. There is no pore at this point of union of the canals nor at any other place between the fourth and fifth supra-orbital organs. The first four organs are innervated by the r. ophthalmicus superficialis facialis, the fifth by a twig arising from the dorsal lateralis ganglion of the facialis just caudad of the origin of the r. oticus, which also supplies a row of large pit organs (Fig. 1, *a. l.*) which continue the direction of this canal caudad and mesad and which agrees closely with the anterior pit line of ALLIS' descriptions of *Amia*. This short canal is present in identically the same relations as regards position and innervation as in *Amia* (ALLIS, '89) and in the siluroids described by POLLARD ('92); viz. *Clarias*, *Auchenaspis*, and *Chaetostomus*, save that in these siluroids it arises from the supra-orbital canal in front of its point of union with the infra-orbital, and in *Clarias* its terminal pore is pushed back a short distance into the squamosal. *Batrachus* has a single sense organ in the corresponding position and with the same innervation (CLAPP, '99), though here it is not enclosed in a canal, and a similar pit line has recently been described in *Polypterus* (ALLIS, '00). In all of POLLARD's cases this organ is innervated by a separate twig arising, as in *Ameiurus*, directly from the ganglion. In *Clarias*, *Callichthys* and *Chaetostomus* POLLARD states that the separation of supra-orbital and infra-orbital canals takes place in the postfrontal bones instead of the frontal, as here. The supra-orbital canal does not communicate with any other canal, nor

does it show any vestige of the frontal commissure as given for *Chaetostomus* and *Clarias* by POLLARD.

*b. The Infra-orbital Canal.* This canal, after its separation from the supra-orbital, runs forward and outward for a short distance still enclosed in the frontal bone. No sense organ is contained in this portion of the canal. It then enters the last (7th.) bone of the suborbital series. In this bone there is neither sense organ nor pore, nor is there a pore between it and the frontal bone. The seventh and last pore of this canal lies between the sixth and seventh suborbital bones and the remainder of the canal passes through six suborbital bones (mostly very slender, mere drain-pipe bones to support the canal) all of which are separated by dermal tubes and surface pores and each of which bears a single sense organ. Following McMURRICH ('84, p. 278), I reckon the lachrymal (his adnasal) as the first bone of the suborbital series.

All of the organs of the infra-orbital canal, as well as adjacent small pit organs are innervated by the r. buccalis, which also supplies the row of large pit organs running transversely in the vicinity of the anterior nasal aperture. Fig. 1 gives the arrangement of these latter sense organs, which have been previously mentioned by ALLIS ('97, p. 629) as occurring in *Ameiurus catus* and *Silurus glanis*.

*c. The operculo-mandibular canal.* In the specimen figured this canal does not communicate with the other canals of the head but is independent for its entire extent. It begins at the tip of the mandible with a pore situated a little laterally and in front of the mental barblet. It immediately enters a canal in the dentary bone, within which there are four sensory organs, all separated by dermal tubules, the fifth tubule running out between the dentary and articular bones. The latter bone contains one sense organ and no pore, though there is a pore immediately behind it. The canal at once enters the preoperculum and here bears three organs, all separated by pores, and terminates by a pore at the caudal end of the preoperculum. The operculo-mandibular canal is accompanied by a row of large pit organs which, like the canal organs, are innervated from the



r. mandibularis externus facialis and which clearly resemble the similar organs on the operculum and mandible of *Menidia* and many other teleosts. I have found no organs in the cat fish corresponding to those on the operculum innervated by the r. opercularis superficialis VII in *Menidia*.

On the right side of the specimen figured the relations of the opercular canal are somewhat different. The preoperculum extends somewhat farther dorsally and the canal runs out from its tip toward the main canal, terminating by a pore very near to the first pore of the main canal, which runs out through the squamosal bone. There is, however, no communication with the main canal. This long portion of the opercular canal which extends dorsad and caudad from the end of the preoperculum runs close under the skin and is enclosed in a very slender tubular ossicle which articulates to the free end of the preoperculum and lies embedded in the dermis, separated from the underlying hyomandibular bone by muscle. Its dorsal end is free.

In two other specimens of which I have transverse sections the relations are still different. In these specimens the arrangements are the same as in the one figured except at the caudal end of the opercular canal, which joins the main canal between the first and second sense organs within the squamosal bone. The preoperculum extends much farther dorsally than in the other case and the canal extends dorsally and caudad from it with no bony investment, embedded in the dermis, to a wide pore by which it communicates with the surface about midway between the preoperculum and the squamosal. This is a double pore corresponding to pore *IX* operculo-mandibular and pore *I* of the main canal of Fig. 1. Between this pore and the squamosal the canal is invested by a feebly ossified incomplete bony ring which is unconnected with any other bone save the squamosal at its dorsal end. The course of the canal between the preoperculum and the squamosal in these two specimens is indicated on Fig. 1 by dotted lines.

The slender investing bones enclosing the opercular canal between the preoperculum and the squamosal are the supraopercular bones, termed by AGASSIZ the supra-temporale, but

not to be confounded with the supra-temporal bones lodging the supra-temporal cross-commissure of the lateral canals. In view of this ambiguous usage it is better to follow STANNIUS and call the latter the extra-scapular, avoiding the term supra-temporal altogether. A single supra-opercular bone is described and figured for *Salmo salar* by BRUCH ('75), and in the next sub-section we shall see that their relations in the American siluroids are exceedingly various.

*d. The main canal.* The main canal runs back for a short distance in the frontal bone, then enters the postfrontal and squamosal. Although its course in the postfrontal is quite long, there is no sense organ contained in this bone, nor is there a pore at its union with either the frontal or squamosal, these two sutures being very firmly united. In the squamosal segment of the canal there are two organs, the first and second of the main line, with a long dermal tubule between them, which is directed outward and forward and opens by pore *I* of the main canal over the lateral edge of the squamosal bone. In the two other specimens of which I have sections the opercular canal joins the main canal in the position of this tubule and the pore is fused with the last pore of the opercular canal. There is a second pore of the main canal behind the squamosal. Then follow four ossicles, each containing a single sense organ and all separated by dermal tubules and pores. The second ossicle clearly is the post-temporal (Fig. 1, *PT*) sometimes called the supra-scapula and termed supra-clavicula by McMURRICH ('84, p. 301), JAQUET, ('98, p. 137) and JUGE ('99),—presenting the characteristic articulations with the cranium and with the vertebral column as described by McMURRICH.

The first one of these ossicles is a slender scale-like bone, closely wedged in between the post-temporal and the squamosal and carrying the canal along its entire length. It is minute but well ossified with a cancellous structure (Fig. 1, *ESC*). This bone is not mentioned in McMURRICH's account of the skeleton of *Ameiurus* ('84), nor in any other work on siluroid osteology accessible to me, and its interpretation is a matter of some difficulty. It appears in all of my specimens of *Ameiurus melas*

and, as we shall see in the next sub-section, it is present in some, but not all, of our other common North American siluroid fishes. In *A. nebulosus* it is present in some individuals, but absent in others. The only bone in this region belonging to the lateral line system which I find described in the literature is the extra-scapular, or supra-temporal. But this bone, or chain of bones, as the case may be, as has been clearly brought out by ALLIS ('99), is characterized by the presence within it of the supra-temporal cross-commissure of the lateral line canal system, and this commissure is totally wanting in all of the North American siluroids which I have examined, as appears beyond. This of course makes it difficult to compare this ossicle with the extra-scapular, and yet the difficulty is not, perhaps, an insuperable one. For in *Amia*, where there is a single extra-scapular bone, the main canal traverses its base and contains within it a sense organ (the 18th. infra-orbital of ALLIS' nomenclature), while the supra-temporal commissure occupies the transverse limb of the same bone. In *Gadus* (COLE, '98), where there are several bones in the extra-scapular series, the main canal traverses the outer one, containing within it a sense organ, and the same is true in *Polypterus* (ALLIS, '00) and in *Salmo salar* (BRUCH, '75). It appears to be probable, therefore, that the ossicle in question corresponds to the lateral extra-scapular or supra-temporal bone of these fishes, the other bones of the series having disappeared with the loss of the commissural canal.

Behind the post-temporal bone there are two (three in one of my specimens) essentially similar tubular bones (Fig. 1, *LOS. 1* and *LOS. 2*), as mentioned above, each carrying one organ of the lateral line. They are long and slender, scarcely larger than the membranous canal which they enclose, and lying free in the sub-dermal tissue. Caudad of this point the canal lies embedded in the dermis at the level of the inter-muscular septum between the dorsal and lateral musculature. Its lumen is much less than that of the cranial canals. The sense organs are arranged in the canal quite regularly throughout the trunk and between each two organs the canal communi-

cates with the surface by a short tubule, passing directly outward through the dermis.

There is an irregular line of large pit organs near the dorsal median line of the trunk, the first four organs of which are indicated at *d. l.* on Fig. 1. These are all innervated from the *r. lateralis vagi* and evidently correspond to the dorsal pit line of *Amia* (ALLIS, '89) and *Batrachus* (CLAPP, '99) and to the row of pit organs in the corresponding position in *Gadus*. The scattered naked neuromasts described above in connection with the *r. lateralis vagi* which accompany the course of the lateral line of the trunk appear to correspond to the accessory lateral lines which have been found by numerous observers accompanying the lateral line of various fishes, for example *Fierasfer* (EMERY, '80). Among the siluroids EIGENMANN ('90, p. 315) describes an extreme form of this in the South American form *Hypophthalmus*, where accessory lateral lines intersect the main lateral line so as to form a lattice-work.

In *Ameiurus melas* the canal systems of the two sides of the body do not communicate by means of commissures at any point. The row of large pit organs across the premaxillary corresponds in position to the premaxillary and ethmoid commissure of *Polypterus* (ALLIS, '00) and of some other fishes. The short segment of the supra-orbital canal leading to pore V and the related anterior pit line (*a. l.*, Fig. 1) may represent a vestige of a similar commissure. There is no occipital or supra-temporal canal, nor is there any vestige of such a canal, unless the occasional presence of the minute extra-scapular bone discussed above is to be regarded as such. And in none of the forms which I have examined is there a pit line which can be identified with the posterior pit line of ALLIS, which in several recorded instances accompanies the occipital commissure. But there is in nearly all specimens of North American siluroids which I have examined either microscopically or macroscopically a well marked pit line consisting usually of two large pit organs on each side forming a transverse line across the top of the head a very short distance caudad of the union of the opercular canal with the main canal in the squamosal (or the first

pore of the main line, when this union does not occur). These organs are innervated from the glossopharyngeus and correspond exactly with the middle pit line of *Amia* (Fig. 1, *m. l.*).

Regarding the structure of the canal organs I have nothing to add to the many previous descriptions of these organs. Those of *Ameiurus* conform to the usual teleostean type, such as COLE figures for *Gadus* ('98, Fig. 4) and I have figured for *Menidia* ('00, Fig. 416). A very unsatisfactory figure of a canal organ of *Ameiurus catus* is given by WRIGHT ('84, Fig 7, Plate I) and the late Dr. BUNKER ('97) thoroughly investigated the nerve terminations in the lateral canal organ of *Ameiurus nebulosus* (*A. catus*) finding the nerve fibers to terminate in free basket-like arborizations around the pear cells, just as in the sense organs of the internal ear.

## 2. *Comparison of lateral line canals of other siluroids.*

*Review of the Literature.*—A comparison of the arrangements just described with POLLARD's account ('92) of African and South American siluroids, notably *Clarias* and *Auchenaspis*, shows a general agreement which is rather close in matters of morphological importance, though there is considerable variation in details. All of these forms agree also quite closely (except in the operculo-mandibular canal) with *Chaetostomus*, a heavily armored and probably very ancient form. This gives POLLARD ground for the assumption that the siluroid type of lateral line is exceedingly primitive, a conclusion which he supports by a comparison with PANDER's figure of the Devonian form *Coccosteus*. In all of POLLARD's cases (*Clarias*, *Auchenaspis*, *Chaetostomus*, *Callichthys*, *Trichomycterus*) the first organ of the main line is supplied by a r. oticus, arising separately from the ganglion, as in *Ameiurus* and the second organ by the IX nerve.

POLLARD attempted to determine the homologies of each of the organs and pores among the five species of siluroids examined by him and with *Amia*, as described by ALLIS. It is an open question how far into detail such homologies can be pushed with profit. In particular, POLLARD's suggested

homology of certain branches of the infra-orbital canal leading out to pores with pit lines in *Amia* is insecure ; for (in addition to the objections raised by ALLIS, '97, p. 629) these pit lines are innervated in *Amia* by branches of the r. hyomandibularis, and not by the r. buccalis, as they should be, if they belonged to the infra-orbital series.

A detailed comparison of the lateral lines of *Ameiurus* and the siluroids described by POLLARD is hardly necessary here, as the salient features can be gathered very readily by a comparison of our figures. Such a comparison, however, brings out very clearly the peculiar and intimate relation existing between the canals and the dermal bones of the skull, a relation which has been recently emphasized by several writers. It is manifest that many of the bones, such as the extra-scapular and the sub-orbital series, have been developed for the canals. Conversely, it is equally evident that the canal is to a large extent dependent (probably as a cenogenetic adaptation) upon the bones and tends to disappear in their absence, as in the case of the infra-orbital line of *Menidia*. This relation between canals and bones is, however, not an inflexible one, as evidenced, for example, by the fact that, even among the siluroids, the supra-orbital and infra-orbital canals may separate either in the frontal or in the post-frontal, and still more clearly by the presence of a canal and a sense organ in the inter-operculum, as well as the pre-operculum, of *Chaetostomus* (POLLARD) and of *Clairas*, according to COLLINGE ('95, p. 277). Moreover in cases where the dermal skeleton is greatly reduced, while the sensory organs of the lateral line system do not suffer a corresponding reduction, as in *Lophius*, the canals disappear and the courses of the lateral lines, as indicated by the rows of naked sense organs, cease to be dependent upon the positions of the underlying bones. For instance, it appears from the careful descriptions and figures of GUITEL ('91) that the opercular line of *Lophius* has been displaced far backward, so that instead of lying over the pre-operculum, it lies over the operculum and sub-operculum. *Batrachus* (CLAPP, '99) exhibits some interesting transitions toward the conditions found in *Lophius*.

ALLIS in his earlier paper ('89) incidentally referred to the lateral canals of *Ameiurus catus* and states that the opercular canal does not communicate with the main canal. WRIGHT ('84, p. 264) says that in *A. catus* there is an occipital commissure just cephalad of the post-temporal bone by which the main canals of the two sides communicate and that this commissural canal bears two pores near the middle line. McMURRICH ('84 a, p. 271), likewise describing *A. catus*, says of the supra-occipital bone, "Posteriorly on each side of the fontanelle, it presents many minute foramina, belonging to the system of mucous canals." The inference from these descriptions is that in *A. catus* there is a supra-temporal canal running in the occipital bone, a condition which I do not find in any of the types examined by me. WRIGHT in the passage cited asserts that the opercular canal does not communicate with the main canal. COLLINGE, describing the lateral canals of *Ameiurus catus*, affirms ('95, p. 279) that there is such an occipital commissure across the mid-dorsal line (without, however, giving any description of it); and also that there is a free communication between the opercular and main canals, and he figures a series of "four small drainpipe-like canal bones, which pass from the region of the posterior border of the hyomandibular bone to the lateral border of the frontal (Pl. XVIII, fig. 3, c. b.) Passing from the main canal into this series of canal-bones, and through the external portion of the hyomandibular bone, the canal enters the preoperculum; from here it passes into the distal portion of the quadrate and then into the mandible, opening by four pores in its course." There are several anomalies in this description to which we shall have to return later. I may now merely mention in passing that in this figure the bone marked sub-operculum is of course the inter-operculum the sub-operculum of siluroids, as is well known, being represented in the first branchiostegal ray. Finally ALLIS ('97, p. 632) acknowledges his error in the matter of the connection between the opercular canal and the main canal in *Ameiurus* and adds, "As I find the canal in *Silurus glanis* as he gives it in *Amiurus*, he is undoubtedly correct."

The discrepancies in the descriptions above referred to and also uncertainty in my own mind as to the true significance of the small ossicle which I find in *A. melas* between the squamosal and the post-temporal have led me to examine these features in such North American Siluridae as are available. A number of the North American cat fishes were examined by dissection as follows:

*Ameiurus melas*, JORDAN and COPE. This dissection of a large specimen of the species used for the microscopical study was made for purposes of control. The specimen, which was 14 cm. long, was examined with a hand-lense, and all of the pores of the canals located. The arrangements of these is indicated in the sketch (Fig. 14), as well as the positions of some of the large pit organs, though not all of the latter could be definitely fixed, especially in the less pigmented areas. The lateral canal of the trunk runs as far back as the level of the ventral fins. Behind this there are more obscure indications of the lateral line, suggesting that the sense organs extend still farther, though even these indications disappear before the base of the tail fin is reached. Behind the shoulder girdle there is but one tubular ossicle (corresponding to the bone *L. OS. 1* of the sections), and that feebly developed. The lateral line ossicle in front of the girdle (*ESC.*) appears exactly as I find it in the sections. There is no occipital commissure of the canal system, and the two large pit organs forming the middle pit line (Fig. 14, *m. L.*) are found in their proper positions.

The opercular canal joins the main canal in the squamosal bone. From the point of union it runs downward and forward, passing directly from the squamosal into a well developed tubular ossicle (supra-opercular bone) which is long and very slender, but firmly ossified, lying under the skin and over the muscles. The double pore (*I* of the main line and *IX* of the operculo-mandibular) opens immediately beyond this ossicle, and the canal continues in the same direction as before without osseous support. This membranous portion crosses the head of the opercular bone, where it articulates upon the hyomandibular, and enters the dorsal tip of the preoperculum,



which it transverses in the usual way. The latter bone is very slender, scarcely more than an investment of the canal, and for its entire length is firmly ankylosed to the hyomandibular. The operculum and interoperculum, on the other hand, are freely moveable.

Upon comparison of this specimen with those examined microscopically it would appear that the union of the opercular canal with the main canal is typical for this species, and that the failure to connect in the case of the specimen plotted is due to retardation of development or to some other exceptional cause. The cheek line of pit organs shown on the figure between the opercular canal and the sub-orbital canal was observed also in a large specimen of *A. nebulosus*. It is represented on the plot (Fig. 1) by the last five or six of the large pit organs accompanying the opercular canal. These all lie dorsally of the canal, the caudal end of the line farther dorsal, but not elevated so far as in the specimen shown in Fig. 14. That is, in the specimen plotted the cheek line of pit organs is not so obliquely placed, but more nearly parallel with the opercular canal.

*Ameiurus nebulosus*, LESUEUR. This is the *A. catus* of most authors, but not of LINNAEUS, the latter's type being probably the channel cat of the Potomac (*A. albidus*, JORDAN), according to JORDAN and EVERMANN. The courses of the lateral canals of the head were dissected out in two small adults from 20 to 30 cm. long. Without going into the details of the sense organs and pores, it may be said at once that the arrangement is in general as I have described it above for *A. melas*. The infra-orbital canal arises at a pore which lies very close to the second supra-orbital pore (the two pores opening within 2 mm. of each other behind the anterior nasal aperture) but the supra-orbital and infra-orbital canals do not anastomose in my specimens as COLLINGE describes and figures ('95, Plate XVIII, Fig. 2) for this species. These two canals join within the frontal bone and the supra-orbital is continued backward to end at a pore corresponding in position to pore V supra-orbital of my figure of *A. melas*. Surface examination shows that there

are behind this pore three large pit organs, corresponding exactly to the line *a. l.* of the figure just referred to.

The osseous support of the opercular canal is more complete than in *A. melas*. Between the mandible and the preoperculum there is a rather long interval. The ventral end of the preoperculum slips under the quadrate, carrying the canal and causing it to appear as if the canal passed through the quadrate. Such is, however, not the case. From the dorsal end of the preoperculum the canal passes through a chain of three tubular ossicles, or supra-opercular bones, to the squamosal, within which it unites with the main canal. None of these tubular ossicles in my specimens was found to be joined to the hyomandibular bone. The main canal between the squamosal and the post-temporal is wholly membranous, the accessory ossicle *ESC.* not being present. Behind the post-temporal there are several drainpipe-like ossicles, then the canal becomes incomplete, as COLLINGE describes. In my specimens I have been able to find no trace of an occipital commissure connecting the main canals of the two sides, such as COLLINGE figures, nor any other connection across the median line. On the surface, however, the middle pit line is obvious in the same relations as in *A. melas*.

A larger specimen 37 cm. long shows important variations. There are but two supra-opercular ossicles. These are both very long and the double pore (*I* of main canal + *IX* of the operculo-mandibular) lies between them. The ossicle *ESC.* is present in exactly the same relations as shown by my sections of *A. melas*. It is a firmly ossified cancellous bone about 7 mm. long, club-shaped, with the larger end fitting closely into the acute angle formed by the articulation of the dorsal limb of the post-temporal with the cranium. There is no appreciable interval between it and the cranium, but behind it the canal is unprotected for some 6 mm. before entering the post-temporal bone. Behind the latter there is but one tubular accessory ossicle and this is very thoroughly ossified. In this specimen, as in the smaller ones, there is no communication between the supra-orbital and infra-orbital canals near the nasal apertures,

though the terminal pore of the infra-orbital canal lies only 1 mm. from the second supra-orbital pore.

*Ameiurus catus*, L. This is the channel cat of the Potomac, or white cat fish, and I am indebted for a fine specimen 32 cm. long, from Beecher Point, Fla., to the U. S. Fish Commission. The lateral line canal is conspicuously present the whole length of the body to the base of the tail fin. The canals of the head were not fully dissected out; but the surface indications, so far as observed, are similar to those of *A. nebulosus* of the same size. The temporal region was, however, carefully dissected and the conditions here found to be identical with those of the large specimen of *A. nebulosus* last referred to. The opercular canal joins the main canal through two similar tubular bones and the course of the main canal through the squamosal, extra-scapular and post-temporal is likewise the same.

*Leptops olivaris*, RAF. (*Pilodictis olivaris*, JORDAN and GILBERT). In a small specimen of the mud cat fish 17 cm. long I find the lateral line canal of the body complete from the head to the tail. It is a very minute canal embedded in the dermis. No small accessory ossicles behind the post-temporal were observed. The main canal of the head passes through the post-temporal bone, then after a short course in which it is not enclosed by the bone it enters the squamosal. Within the squamosal the main canal is joined by the opercular canal. The latter passes downward and forward for a short distance in the squamosal bone, then over the most caudal edge of the hyomandibular bone, just cephalad of opercular bone, to enter the dorsal edge of the preoperculum. The extent of the canal dorsally of the preoperculum is somewhat longer than that within the preoperculum and this portion is enclosed by several very delicate supra-opercular ossicles which may be either incomplete rings or tubular bones entirely enclosing the canal. The first is a long bone of the latter type and quite free from other bones except at its ends. Then follow one or two ossicles which are partially or wholly incomplete externally, while the last one wholly encloses the canal. All of these except the first are firmly co-ossified to the hyomandibular bone and

doubtless the specimens of *Ameiurus catus* which COLLINGE examined exhibited a similar peculiarity, for he says that the canal in that species runs through the external portion of the hyomandibular, a form of statement which is hardly admissible in view of the fact this bone belongs to the primordial cranium. In COLLINGE's description he adds that from the preoperculum the canal "passes into the distal portion of the quadrate and then into the mandible." It is obvious in all of the forms which I have examined that the canal has no relation to the quadrate, though in this instance the preoperculum, quadrate and hyomandibular are very intimately joined. The course of the canals in front of the eye was not dissected out.

*Ictalurus punctatus*, RAF. The heads of two large specimens of this species were partially dissected and the arrangements so far as studied correspond quite closely with those just described for *Leptops*. The head is much narrower and higher than in *Leptops* and the preopercular bone extends much farther dorsally so that the opercular canal is enclosed in this bone for about three fourths of the distance between the squamosal bone and the mandible, instead of less than one half, as in *Leptops*. From the post-temporal bone the main canal passes into the squamosal without being enclosed by a separate ossicle. Within the squamosal bone the opercular canal joins the main canal and, as before, passes for a short distance through this bone, directed forward, outward and downward toward the operculum. In the interval, in my specimens about 1 cm., between the squamosal and the dorsal tip of the preoperculum the canal is enclosed by a single very slender supraopercular ossicle. The remainder of the canal is deeply embedded in the preoperculum nearer its cephalic than its caudal margin. As in *Leptops*, the preoperculum is immovably co-ossified with the quadrate and the hyomandibular for its entire length. The operculum and interoperculum, on the other hand, are freely movable.

*Noturus flavus*, RAF. Two examples of this species about 18 cm. long were dissected. The opercular canal is connected with the main canal, enclosed by one or more slender tubular

ossicles between the dorsal end of the preoperculum and the squamosal. These ossicles are distinct and well formed, but in texture are more like a jointed investment of connective tissue, for they are slightly or not at all calcified. This same remark holds true for some of the specimens of other species dissected, though to hardly so great degree. The portion of the canal between the squamosal and the post-temporal is longer in this species than in any of the others examined. The investment of the canal here is likewise of very dense, well defined connective tissue, but not clearly ossified. There is no occipital commissure of the canal system.

It is worthy of remark that the North American siluroid fishes comprise a very close group and that the forms here described are all closely related. The species, and even genera, are distinguished by very trivial characters and transitional forms are very abundant. It is obvious that if slight variations in the degree of development of the lateral line canals may involve, as in these cases, so important skeletal changes in closely related species (and even among individuals of the same species) as the development or suppression of several distinct cranial bones, then such of the bones of the head as are formed in connection with the lateral line canals must be used in morphological and phylogenetic speculations with great caution and with allowance always made for this surprising variability. This series of forms also illustrates in an interesting way how elements of the primordial enchondral cranium may secondarily assimilate dermal elements. In one specimen of *Ameiurus melas* no lateral canal or ossicles are developed dorsally of the preoperculum. In other forms there is a canal in this position enclosed in one or more separate dermal ossicles. And finally in *Leptops* several of these ossicles have fused with the underlying hyomandibular bone very intimately.

*Menidia.* In the light of these relations I have re-examined the bone of *Menidia* which I have termed the extra-scapular, marked *ESC* on Fig. 5 of my *Menidia* paper ('99). This bone carries the main canal caudad of the squamosal and also the short branch which represents the supratemporal or occipital

commissure. It may, therefore, represent both the post-temporal and the extra-scapular fused, though I find no direct evidence of such fusion. Fig. 1 of the paper referred to shows this bone (marked *E. S.*) just cephalad of the point of separation of the commissural canal from the main canal. The commissural canal extends practically no farther mesially than here indicated, but the dorsal limb of the bone continues much farther, articulating with the cranium not far from the median line over the point of union of the posterior and anterior semi-circular canals (Cf. Fig. 5, loc. cit.). The bone has the characteristic Y-shape and the ventral limb (shown in Fig. 1 referred to above ventrally and mesially of the lateral line canal) articulates with the skull far ventrally of the other articulation. The caudal limb articulates with the shoulder girdle in the usual way and carries the main lateral line canal to its tip. The bone as a whole should therefore unquestionably be called the post-temporal.

### 3. *The pit organs.*

Fig. 12 illustrates a section taken through the middle of a typical *small pit organ* stained by WEIGERT's method after fixation in FLEMMING's fluid. The structure is essentially similar to that of the canal organs, with large pear cells among the indifferent supporting cells. I have not noticed in my preparations a cupula, or debris of cilia over these organs, but quite probably the cilia occur, as the prolonged treatment in FLEMMING's fluid which my specimens received is not favorable for the preservation of such structures. The aperture by which the pit communicates with the surface is a very minute pore, round or nearly so, not a slit as in the case of some ganoid fishes and of the pit organs of *Ameiurus catus* as described by WRIGHT ('84, p. 267). The latter author gives a description in the passage cited of pit organs in young *Ameiurus catus* which corresponds very closely to what I find here. In the specimen which I figure here the pit seems to have shrunk inward somewhat under the influence of the reagents. Normally the pore opens out on unmodified body surface, which is

neither elevated nor depressed at that point, and the pore may run downward as a straight tube of considerable length before dilating into the sac-like cavity of the pit. Glandular, or mucous, cells and the clavate cells of Leydig are found in close proximity to the pits, as in the case of the terminal buds, and I have not been able to locate these small pits by surface examination of either fresh or preserved specimens of any species.

These pits are exceedingly numerous and tend to be arranged in rows or lines, though this arrangement is usually not noticeable. To map them accurately would be very laborious and I have not attempted it. In very young specimens this will doubtless prove not only easy, but much more fruitful in morphological suggestion. They are freely scattered over almost the whole body surface, but much more plentiful on the head than on the trunk. They are in general perhaps more abundant in the neighborhood of the canals and lines of large pit organs, but not conspicuously so. Their nerve fibers are of medium size, but their medullary sheaths are exceedingly feebly developed, so that the innervation of the organs can be traced with great difficulty, even in good WEIGERT sections.

The organs which I here term *large pit organs* resemble quite closely those which I called pit organs in my accounts of *Menidia* and the young cod fish which formed the subjects of my previous memoirs. These organs generally appear in my sections to be strictly superficial, usually projecting slightly above the surrounding surface, and they are commonly very conspicuous upon surface examination by reason of the absence of pigmentation around them. They rest on unmodified corium or the dermis may be slightly elevated under them, especially around their edges, thus forming a sort of saucer-shaped elevation upon which the cells of the sensory organ rest. The shape of the organ is that of a broad dome with a flat base which rests directly upon the chorium. The epidermis becomes thinner as the organ is approached and its margin overlaps the base of the organ, a shallow circular groove on the surface marking the contact of the non-sensory epidermis with the sense organ. The organ projects above the surface of the surrounding epi-

dermis by about one-fourth of its thickness. The nerve penetrates the corium under the middle of the organ, its fibers losing their medullary sheaths and spreading out over the lower surface of the sense organ. The specific sensory cells, or pear cells, are crowded rather closely in the narrow outer portion of the dome-shaped organ and they extend inward about one-third of the thickness of the organ. The exposed surface of the organ is covered with a dense external limiting membrane which is continuous with that of the surrounding epidermis and upon which is a more or less indistinct coagulum which may represent vestiges of cilia. This is the type of large pit organs most often observed in my sections of *Ameiurus*; but some of larger organs present a more elaborate structure.

In these cases the organ is sunken below the surface of the surrounding epidermis and separated from it by a rather deep circular groove, some modified epidermal cells on inner side of the groove arching in the form of a lip over the edge of the free ends of the sensory cells. Fig. 13 shows a section taken somewhat to one side of the middle of such an organ. In a section taken through the middle of the organ, the patch of sensory epithelium is considerably wider and a proportionately smaller part of the exposed surface is overlapped by this lip. The nerve is there likewise seen to pierce the corium and enter the center of the organ very much as it appears in the small pit organ, Fig. 12. The nerve fibers for the large pit organs, unlike those for the small pit organs, are large and densely medullated, appearing in the sections much like those for the neuromasts in the lateral line canals.

Surface examination with a lense of the larger specimen of *A. melas* shown on Fig. 14 gives a quite different impression of these organs. They appear as slightly elevated spots rather conspicuous by reason of the total lack pigment. They are rarely circular, but more often a raised line runs out at opposite ends of a diameter of the disc as shown in the figure. When the organs are arranged in definite lines they are frequently connected by a continuous raised line in this way. Commonly no pore is visible at the apex of the papilla in alcoholic specimens,



though in a large specimen of *A. melas*, whose pit lines present the same appearance as here described, a slit-like pore is occasionally seen. Upon inserting a probe a capacious cavity is discovered roofed by a thin non-pigmented membrane and floored by the sensory epithelium. I infer that the strictly naked type first described is an imperfectly developed or immature stage of this kind of large pit organ.

Unlike the terminal buds, these organs are wide at the apex, which is often flat topped. The base is still wider by reason of the fact that the nuclei of the supporting cells are near their bases. The supporting cells are usually more darkly stained by the treatment given than are the cells of the surrounding epidermis. Pear cells are found in the organ in essentially the same relations as in the other neuromasts, or organs of the acustico-lateralis system, though in this case they are usually much smaller than in the others. They extend scarcely one-third of the way from the apex to the base of the organ, and are frequently stained very pale, often invisible altogether, whereas in the canal organs and small pit organs the pear cells are always conspicuous and often much darker than the supporting cells. The general arrangement strongly suggests the figures given by KINGSBURY ('95) for the naked lateral line organs of Amphibia, notably *Diemyctylus*. In my sections of *Menidia* and *Gadus*, which were prepared by essentially the same method as these of *Ameiurus*, I was not able to demonstrate any pear cells in the corresponding pit organs, though it is quite possible that suitable technique would show them up. But Miss CLAPP's sections of the sense organs of the lateral lines of *Batrachus*, which are not open to such technical limitations, likewise do not show pear cells sharply differentiated from the supporting cells, and this applies, if I understand her correctly, to both the naked neuromasts and those contained within the lateral line canals. The significance of the pear cells in these neuromasts requires further study. It is clear, at any rate, that the pear cells are typically present in all organs of the lateral line series, or neuromasts, and that MERKEL's ('80) distinction between these organs and the terminal buds is morpho-

logically valid, and that too apart from the fact (of which he was apparently ignorant when he established the distinction) that the two types of organs are innervated by totally distinct nerve components, acustico-lateralis, on the one hand, and communis on the other. That neuromasts by reason of degenerescence, change of function, or some other cause, may sometimes secondarily lose their pear cells is quite possible; but now that we know the innervation of these organs and have reason to believe that the nerve supply is invariable (i. e., that neuromasts are always innervated by acustico-lateralis nerves and terminal buds by communis nerves) it is possible to determine to which class any set of organs belongs independently of the presence or absence of pear cells, if only their innervation can be worked out.

A comparison of the organs of the lateral line system of *Ameiurus* with those of other fishes shows clearly that the groups of naked neuromasts which I termed "pit lines" in *Menidia* and *Gadus* correspond to the large pit organs of *Ameiurus*, and not to the small pit organs of this fish. It would appear that those fishes do not possess anything comparable with the small pit organs described in the present contribution. Possibly embryological study will shed some light upon the significance of the three types of neuromasts here described, and pending such an examination speculation upon these subjects may as well be deferred until we have more facts at command.

ALLIS ('97, p. 629) mentions in *Ameiurus catus* the row of naked neuromasts across the tip of the snout and "two or possibly three lines on the top of the head." One of these is clearly the line continuing the supra-orbital canal caudal of its fifth pore of my account; the others are not described. He terms these organs "pit organs" but does not describe their structure. I find no evidence that he has ever seen the organs which I have termed small pit organs in this paper.

## SUMMARY AND CONCLUSIONS.

This study was undertaken primarily to discover the distribution, structure and innervation of the cutaneous sense organs of the common American cat fish preliminary to an embryological research upon these organs, the corresponding nerve components and their cerebral centers. In the course of this work the components of the cranial nerves have been worked out in detail and plotted, and thus our knowledge of the exact composition of the nerves of the head is extended to another vertebrate type. The chief points of morphological importance which this study has yielded are as follows:

1. The composition of the cranial nerves of *Ameiurus* is substantially the same as that of the other teleostean fishes whose nerves have been thoroughly worked out. The trigemino-facial ganglionic complex is much more compact and intricate than in teleosts in general, but it presents no fundamental differences in plan. The other cranial nerves are also of the typical teleostean type, save the eye-muscle nerves, whose arrangements conform to the ganoidean pattern so far as this latter is at present known (Allis, '97, Workman, '00). The central termini of these components are strictly typical as compared with other vertebrates, save that the enlargement of the communis component of the facialis has resulted in the development of a special terminal nucleus of large size for these fibers at the cephalic end of the fasciculus communis, the lobus facialis. Peripherally the components have the typical distribution. Thus, of the motor components, the somatic motor innervates only somatic muscles and the visceromotor only those commonly relegated to the visceral musculature; the general cutaneous system supplies the skin only, never specialized sense organs; all taste buds and terminal buds, wherever distributed over the body, are supplied from the communis system; and the acustico-lateralis system innervates only specialized sense organs, or neuromasts, of a definite type of structure which is different from that of the terminal buds. All of these sense organs are very highly developed, and this case furnishes an absolute

demonstration of the anatomical distinctness of the two chief types of special cutaneous sense organs and of their nerve supply.

2. MERKEL'S distinction between neuromasts (*Nervenhügel*) and terminal buds (*Endknospen*) will stand, the former being typically furnished with pear cells, or hair cells, which are shorter than the other cells of the sensory epithelium and which receive the specific nerve termini. To this structural difference we can now add the difference in their innervation, the neuromasts always being supplied by nerves of the acustico-lateralis system, the terminal buds by communis nerves.

3. Terminal buds are distributed over the entire cutaneous surface of the head and trunk, most abundantly on the head; but all are innervated from the communis component of the VII, IX and X cranial nerves, those of the trunk being supplied from the r. lateralis accessorius.

4. There are four types of sense organs belonging to the acustico-lateralis system in *Ameiurus* (1) the organs of the internal ear, (2) the canal organs of the lateral lines, (3) the large pit organs, few in number and corresponding to the familiar pit organs of other teleosts in general and of *Amia*, (4) the small pit organs, not commonly present in other fishes, very numerous and distributed over the whole surface of the head and trunk.

5. There is considerable conflict in the literature regarding the the exact courses of the lateral line canals in the siluroids. Accordingly I have plotted carefully the whole system in *Ameiurus melas* and have also examined by dissection portions of the system in several other American siluroids. There prove to be important variations in the different species, in different specimens of the same species, and even in the two sides of a single specimen. These differences include the presence or absence of a connection between the opercular and the main canals and the presence or absence of accessory ossicles at various points in the canal system, and may account for some of the disagreements in the literature. It follows that the details of the lateral lines and their smaller accessory ossicles are

of slight value either to taxonomy or to phylogeny. It should be noted, however, that all lateral line ossicles are dermal bones specialized for this purpose, and that the canals do not penetrate bones belonging to the primordial cranium, though some recent descriptions have stated this to occur in *Ameiurus*.

6. The bone of *Menidia* which I termed the extra-scapular in my contribution published in 1899 is probably a fusion of the extra-scapular and the post-temporal, since the extra-scapular, as defined by Allis, is a dermal ossification (or several such) developed to carry the supra-temporal commissure of the lateral line canal, while the post-temporal belongs to the shoulder girdle.

7. The composition and distribution of the several nerves need not be reviewed in detail here. The most striking feature is the fusion in many of the cutaneous nerves even to their minute ramifications of two or three of the components, so that their analysis is a matter of extreme difficulty, especially as the components do not differ in the caliber of their fibers so much as in most other fishes. Nevertheless this analysis can be effected in the majority of cases and in the hundreds of sense organs whose innervation has been accurately determined no exception has been found to the laws of nerve supply laid down above.

8. The r. mandibularis internus of the facialis appears to be lacking in *Ameiurus*; for, though the hyomandibular trunk receives some communis fibers, these apparently all distribute to terminal buds of the outer skin of the opercular region and none are continued inward to supply the mucous lining of the mouth.

9. The r. mandibularis externus facialis divides into two portions, an internal one for the mandibular lateral line canal organs, and an outer one, which I have termed the cutaneous branch, for pit organs of both the large and the small variety along the course of this canal. The latter nerve carries both communis and general cutaneous fibers in addition to its proper lateralis fibers. Some writers on siluroid nerves have erroneously called this cutaneous branch the main r. mandibularis externus,

and the deeper branch the r. mandibularis internus, ignoring the fact that the latter nerve is of communis nature.

10. The nerve which in *Menidia* and *Gadus* I termed the pre-trematic branch of the facialis is present in *Ameiurus*. It supplies taste buds in the lining of the suspensorium and of the proximal part of the hyoid arch. The middle and ventral parts of the hyoid arch are supplied from a large recurrent branch of the glossopharyngeus. The taste buds in the lining of the mandible are not supplied from any branch of the facialis, but from a branch of the r. mandibularis V. There is, therefore, nothing in this fish, which could be called a chorda tympani, as I have defined this term in the ichthyopsida, unless it be this nerve. It is more probable, however, that it is one of the branchial nerves, though it has nothing to do with the pseudo-branch in *Ameiurus*. Whether it should be termed the pre-trematic or the post-trematic nerve will depend upon whether the teleostean pseudobranch is a mandibular or a hyoidean demibranch. As this question is still in dispute, I have returned in this paper to the older designation, *posterior palatine* in order not to prejudice its morphological significance.

11. The mandibular and maxillary branches of the trigeminus both receive general cutaneous and communis fibers in approximately equal proportions. The communis component corresponds to the "infero-medial strand" and the general cutaneous component to the "supero-lateral strand" of WRIGHT. All of the barblets apparently receive both general cutaneous and communis nerves, but chiefly the latter. They are very abundantly supplied with terminal buds and doubtless have a function (at present unknown) associated with these organs in addition to their general tactile function.

12. The ophthalmic nerves of *Ameiurus* have been cleared up by my pupil, Mr. WORKMAN, on the basis of the same material as here reported upon. We find that the superficial ophthalmic of authors is the facialis branch of this name and supplies the supra-orbital lateral line canal organs and the associated pit organs only. The nerve which previous writers on the siluroids have termed the ophthalmicus profundus is in reality

the ophthalmicus superficialis trigemini plus a large communis component. This nerve fulfils none of the requirements of an ophthalmicus profundus, and deviates from the conditions typical for the ophthalmicus superficialis trigemini only in that it runs under the origin of the m. dilator operculi. Ameiurus therefore, conforms to the teleostean, rather than to the ganoid type in this respect also.

13. The ramus lateralis accessorius clearly arises wholly or nearly so from the geniculate ganglion of the facialis and throughout its course in the trunk it carries communis fibers from this source only, save for the temporary fusion with it of dorsal rami of the successive spinal nerves. This nerve cannot, therefore, properly be called a "collector" of the dorsal spinal rami, for its connection with these nerves is accidental rather than primary. There are no terminal buds in the trunk which are not reached by fibers from this nerve. Moreover, since all parts supplied by this nerve have an independent general cutaneous nerve supply from the spinal nerves, it cannot be regarded as a "somatic sensory" nerve, or nerve of general cutaneous sensibility. The vagal root of the r. lateralis accessorius is lacking in Ameiurus.

14. The glossopharyngeus has the typical teleostean composition as it leaves the brain, viz. communis and visceral motor. Before leaving the cranium it receives a lateralis component from the vagus whose intra-cranial relations are variable. This nerve forms a r. supra-temporalis glossopharyngei which supplies the second sense organ of the lateral line canal within the squamosal bone and the middle pit line. There is no pre-trematic ramus nor JACOBSON's anastomosis.

15. The vagus has the typical composition. The motor root supplies, among others, the pharyngo-clavicularis muscles and the trapezius muscle. The vagus has the usual general cutaneous component, with its jugular ganglion and r. cutaneus dorsalis. The r. lateralis vagi supplies the lateral canal of the trunk and both large and small pit organs. It does not participate in the innervation of the skin in general or of termi-

nal buds. It is in no sense a "collector" of spinal nerves, being morphologically quite distinct from the whole spinal system.

16. Finally, I would again emphasize the morphological absurdity of all attempts at the homology of sensory nerves belonging to totally different components, as, for instance, to homologize a lateral line nerve with a dorsal ramus of a spinal nerve, or with a pure communis nerve; yet this error is being perpetuated constantly by morphologists of repute. This study is a conclusive demonstration of the morphological discreteness of these sensory components.

*Denison University,  
August 20, 1901.*

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## DESCRIPTION OF FIGURES.

All of the figures illustrating this paper, except Fig. 14, have been drawn from a single series of sections through the head and body of *Ameiurus melas*, prepared by the WEIGERT process, as detailed in the introductory section of this paper.

## REFERENCE LETTERS.

- a.*—general cutaneous root of the r. ophthalmicus superficialis V.
- ac. mx.*—accessory maxillary nerve.
- ac. mx. c.*—general cutaneous root of accessory maxillary nerve.
- a. l.*—anterior pit line.
- a. n. a.*—anterior nasal aperture.
- ART.*—articular bone.
- ASP.*—alisphenoid bone.
- b. v.*—blood vessel.
- c.*—communis root of r. ophthalmicus superficialis V.
- cereb.*—cerebellum.
- cl.*—clavate cells of Leydig.
- com.*—communis root of the facialis.
- com. X.*—communis root of the vagus.
- cut. dors.*—ramus cutaneus dorsalis vagi.
- cut. m. ex. VII.*—cutaneous branch of r. mandibularis externus VII.
- cut. V.*—general cutaneous root of the trigeminus.
- cut. X.*—general cutaneous root of the vagus.
- d.*—dermis.
- D.*—dentary bone.
- d. l.*—branch of r. lateralis vagi for dorsal pit line of trunk.
- d. lat. X.*—dorsal (main) branch of r. lateralis vagi.
- d. l. g.*—ganglion of the dorsal lateral root of the facialis.
- d. l. r.*—dorsal lateralis root of the facialis.
- e.*—epidermis.
- ESC.*—extrascapular (supratemporal) bone.
- F. buc.*—foramen of r. buccalis facialis.
- F. IX.*—foramen of glossopharyngeus.
- F. lat. ac.*—foramen of r. lateralis accessorius.
- F. II. X.*—foramen of the vagus.
- F. os. V.*—foramen of r. ophthalmicus superficialis V.
- F. os. VII.*—foramen of r. ophthalmicus superficialis VII.
- F. ot.*—foramen of r. oticus.
- F. pt. VII.*—foramen of r. palatinus posterior.
- FR.*—frontal bone.
- F. t. hm.*—foramen of truncus hyomandibularis.
- F. t. i.*—foramen of infra-orbital trunk.
- F. 5.*—foramen for nerve for fifth organ of supra-orbital canal.
- gen. g.*—geniculate ganglion.
- g. IX.*—ganglion of the glossopharyngeus.

*g. lat. ac.*—ganglion of r. lateralis accessorius (portion of geniculate ganglion).

*g. lat. X.*—ganglion of r. lateralis vagi.

*HM.*—hyomandibular bone.

*III. s.*—branch of third nerve for m. rectus superior.

*III. v.*—ventral branch of third nerve.

*inf. med.*—infero-medial strand (communis) of infra-orbital trunk.

*I. o. c.*—infra-orbital canal.

*IV.*—trochlearis nerve.

*jug. g.*—jugular ganglion of the vagus.

*lat. X.*—lateralis root of the vagus.

*ll. IX.*—lateralis branch (r. supratemporalis) of the IX nerve.

*lob. inf.*—lobi inferiores.

*lob. VII.*—lobus facialis of oblongata.

*LOS. 1, LOS. 2.*—accessory lateral line ossicles.

*m.*—meningeal twig of r. lateralis accessorius.

*m. ad. arc. pal.*—m. adductor arcus palatini.

*m. ad. t.*—m. adductor tentaculi.

*m. a. m.*—m. adductor mandibularis.

*m. b.*—origin of mental barblet.

*M. c.*—main lateral line canal.

*m. d. o.*—m. dilator operculi.

*m. l.*—middle pit line.

*m. l. a. p.*—m. levator arcus palatini.

*mot. V.*—motor component of the trigeminus.

*mot. VII.*—motor root of the facialis.

*muc.*—mucous cells of the epidermis.

*mx. b.*—maxillary barblet.

*NA.*—nasal bone.

*n. al.*—nerve of anterior pit line (continuing the supra-orbital canal).

*n. b.*—origin of nasal barblet.

*n. mot. X.*—motor nucleus of vagus.

*n. 5.*—nerve of fifth organ of supra-orbital canal.

*obl.*—medulla oblongata.

*ol. b.*—olfactory bulb.

*op. lob.*—optic lobe.

*op. n.*—optic nerve.

*OSP.*—orbito-sphenoid bone.

*o. s. 5.*—fifth organ of supra-orbital canal.

*out. buc.*—outer buccal branch of the facialis.

*o. V.*—superficial origin of the trigeminus.

*o. VII.*—superficial origin of the facialis.

*PFR.*—post-frontal bone.

*pmb.*—origin of post-mental barblet.

*p. n. a.*—posterior nasal aperture.

*POP.*—preoperculum.

- PRO.*—prootic bone.  
*pros.*—prosencephalon.  
*PS.*—parasphenoid bone.  
*PT.*—post-temporal (supra-clavicular) bone.  
*r. ad. man.*—branch of trigeminus for m. adductor mandibulae.  
*r. ad. pal.*—branch of facialis for m. adductor arcus palatini.  
*r. buc.*—ramus buccalis facialis.  
*r. cut. dors. X.*—ramus cutaneus dorsalis vagi.  
*r. hy.*—ramus hyoideus facialis.  
*r. l. a. p.*—branch of r. mandibularis V for m. levator arcus palatini.  
*r. lat. ac.*—ramus lateralis accessorius (r. recurrens facialis).  
*r. lat. X.*—ramus lateralis vagi.  
*r. man.*—ramus mandibularis trigemini.  
*r. man. ext. VII.*—main ramus mandibularis externus facialis.  
*r. max.*—ramus maxillaris trigemini.  
*r. op.*—ramus opercularis profundus (for mm. adductor hyomandibularis, levator operculi and adductor operculi).  
*r. oph. sup. V.*—ramus ophthalmicus superficialis V.  
*r. oph. sup. VII.*—ramus ophthalmicus superficialis VII.  
*r. ot.*—ramus oticus facialis.  
*r. pal.*—ramus palatinus facialis.  
*r. pt. VII.*—ramus palatinus posterior (r. pre-trematicus facialis?).  
*r. s.*—m. rectus superior.  
*r. st. IX.*—ramus supra-temporalis glossopharyngei.  
*r. s. 5.*—buccal branch for fifth organ of sub-orbital canal.  
*s. gel.*—substantia gelatinosa.  
*So. c.*—supra-orbital canal.  
*SO1.*—first sub-orbital bone (or lachrymal, or antorbital).  
*SO2 to SO7.*—second to seventh sub-orbital bones.  
*sp. g. 2.*—second spinal ganglion.  
*sp. V.*—spinal V tract.  
*sp. 1.*—branch of r. lateralis accessorius for ventral ramus of first spinal nerve.  
*sp. 2.*—branch of r. lateralis accessorius for ventral ramus of second spinal nerve.  
*SQ.*—squamosal (pteroic) bone.  
*sup. lat.*—supero-lateral strand (general cutaneous) of infra-orbital trunk.  
*sy.*—sympathetic nervous system.  
*t. a.*—tuberculum acusticum.  
*t. hm.*—hyomandibular trunk.  
*u.*—point of union of infra-orbital and supra-orbital canals.  
*v. lat. X.*—ventral branch of r. lateralis vagi.  
*v. l. g.*—ganglion of the ventral lateralis root of the facialis.  
*v. l. r.*—ventral lateralis root of the facialis.

## PLATE XIV.

*Fig. 1.* Projection on the horizontal plane of the lateral line canals, their nerves and sense organs of the left side.  $\times 28$ . The scales at the top and bottom of the plate indicate millimeters divided into quarters. The root portions of some other parts of the trigeminus, facialis, glossopharyngeus and vagus are indicated in outline, while the lateral line nerves are drawn in black. The brain and olfactory and optic nerves are shaded with stipple. The outline of the eye is indicated by a dark continuous line, and the origins of the nasal, mental and post-mental barblets by heavy dotted lines. The lateral line canals are cross-hatched, their organs are indicated as black rings, while the large pit organs are indicated as black discs. The small pit organs are not indicated. The canal organs and pores are numbered from before backward in each canal (the former in Arabic, the latter in Roman numerals), and the boundaries of the bones through which the canals pass are indicated by heavy curved lines marked by abbreviations of the bones, in capital letters. Regarding the nomenclature of the canals, the supra-orbital canal is regarded as terminating in the fifth supra-orbital pore; the infra-orbital canal terminates at its union with the supra-orbital; and the canal running caudad from this point into the trunk is the main canal. In this specimen the opercular canal does not communicate with the main canal. The relations in two other specimens, in which these canals do communicate, are indicated by dotted lines.

## PLATE XV.

*Fig. 2.* Projection of the sensory trigemino-facial roots on the sagittal plane as seen from the left side.  $\times 65$ . The scales at the top and bottom of the plate indicate millimeters (measured from the tip of the snout) divided into quarters. The outline of the brain is indicated by a heavy continuous line. The communis system is indicated by wide cross-hatching, the lateralis system by narrow cross hatching and the general cutaneous system by stipple. Ganglion cells belonging to the communis system are indicated by  $\times$ , to the lateralis system by  $\circ$  and to the general cutaneous system by  $+$ . Superficial origins of the roots from the brain are indicated by double transverse lines; foramina in the skull by single transverse lines.

## PLATE XVI.

*Fig. 3.* Transection through the head at the level of exit of the optic nerve from its foramen (6 millimeters from the tip of the snout, cf. Fig. 1)  $\times 28$ . In the r. ophthalmicus superficialis V, the r. maxillaris and r. mandibularis the relations of the two sensory components are indicated by the lines dividing these nerves, the general cutaneous component being dorsal and lateral and the communis component ventral and mesial.

This and the following transverse sections, though apparently from the right side, in reality illustrate the left side, the relations having been reversed by the projection.

*Fig. 4.* Similar transection farther caudad (6.6 millimeters from the tip of the snout)  $\times 28$ . The plane of the section is just proximal to the point where the supero-lateral and infero-medial strands are rearranged to form the maxillary and mandibular nerves.

*Fig. 5.* Similar transection farther caudad (at 7 millimeters)  $\times 28$ . At this plane the infero-medial and supero-lateral strands are passing through their foramen in the cranium.

*Fig. 6.* Similar transection farther caudad (at 7.3 millimeters)  $\times 28$ . This level lies at the point of origin of the r. palatinus posterior and immediately cephalad of the origin of the hyomandibular trunk (cf. Fig. 2).

*Fig. 7.* Similar transection farther caudad (at 8.3 millimeters)  $\times 28$ . The section passes through the ganglionic root of the r. lateralis accessorius.

*Fig. 8.* Similar transection farther caudad (at 8.7 millimeters)  $\times 28$ . The section lies just caudad of the superficial origin of the trigeminus from the oblongata.

*Fig. 9.* Similar transection farther caudad (at 10.4 millimeters)  $\times 28$ . Shows the superficial origins of the communis and motor roots of the vagus and the passage of the glossopharyngeus through its foramen in the cranium.

#### PLATE XVII.

*Fig. 10.* Transection similar to the last and still farther caudad (at 10.7 millimeters), passing through the jugular ganglion of the vagus.  $\times 28$ .

*Fig. 11.* Section through a terminal bud in the skin of the top of the head.  $\times 560$ .

*Fig. 12.* Section through a small pit organ in the skin of the top of the head.  $\times 560$ .

*Fig. 13.* Section through a large pit organ from the top of the head, the innermost organ of the nasal pit-line, Fig. 1.  $\times 560$ . The section is taken to one side of the middle of the organ and so does not show the largest extent of the organ nor the nerve supplying it. The small pear cells are seen among the outer ends of the supporting cells and just external to the organ is a "cupula" composed doubtless of disintegrated hairs from the pear cells.

*Fig. 14.* Sketch of the right side of a large specimen of *Ameiurus melas*, showing the pores of the lateral line canals and some of the large pit organs.  $\times 12-5$ .





## THE PSYCHOLOGICAL THEORY OF ORGANIC EVOLUTION.<sup>1</sup>

By H. HEATH BAWDEN, Ph.D.

This paper consists of three parts. The first part is a somewhat metaphysical introduction which, if not clear, at least possesses the merit of being brief. It sets forth certain implications of what is here called the psychological theory of organic evolution. The remainder of the paper is an application of this point of view to the evolution of consciousness in a consideration, first, of the evolutionary conditions of the emergence of consciousness, and, second, of the stages in that evolution.

The aim is to understand the process by which consciousness has been built up. In man, the highest representative in general intelligence of all the mammals, we find a relatively continuous and comparatively well-organized consciousness. Human consciousness is not absolutely continuous.<sup>2</sup> It lapses, for example, in dreamless sleep. Nor has human consciousness reached the highest degree of organization possible, as the imperfections of language alone bear witness. But compared with what we know of the consciousness of the lower animals, the mammals, and especially man, possess a continuity and organization of consciousness not found in the lower forms. Assuming that this complex consciousness, like everything else organic, has resulted from a process of gradual growth, the present inquiry is into some of the conditions and stages of that growth.

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<sup>1</sup> A paper read before the Baconian Club of The State University of Iowa, March 15, 1901.

<sup>2</sup> Though it is self-healing over the gaps.

In the first place, of course, evolution is assumed. Whether this evolution has been catastrophic or uniform need not concern us here. It is sufficient to note that it is gradual, that is, a graded growth.

In the second place, it is assumed that the psychical cannot have evolved from what we call the physical. To suppose that the psychical developed out of the physical is to contradict the scientific law of the conservation of energy. If the psychical grows out of the physical then examination should show that a certain amount of physical energy disappears as physical to reappear as psychical. But science does not find this to be true; the physical is not causally related to the psychical. Whatever the psychical may be, it falls outside physical energy, and science formulates this conclusion in its postulate of psycho-physical parallelism. Science does not attempt to penetrate into the puzzle of the relation of the psychical to the physical; it contents itself with the doctrine of parallelism as a working hypothesis. It finds the psychical as a sort of white elephant on its hands. It cannot deny it and thus get rid of it. Nor can it accept it and incorporate it into itself. Hence science simply says that the physical and the psychical stand side by side, and lets the problem rest there, or hands it over to metaphysics.

But we cannot escape the difficulty so easily here, since our subject involves just this question of the nature of the psychical. We may set aside materialism and spiritualistic idealism and the theory of interactivity, all of which hold to the view that the physical and the psychical are causally related, and confine our attention to this theory of parallelism which professes at least not to contradict any known scientific law. Parallelism is the current doctrine, not only of modern science, but of much modern philosophy. There are two types. One is complete parallelism, holding that the physical and the psychical run parallel throughout. The other is partial, holding that the psychical is parallel to the physical so far as the psychical extends, but that it forms a shorter series than the physical. According to the first theory every psychosis has its neurosis

and every neurosis has its psychosis. According to the second theory every psychosis has its neurosis but not every neurosis has its psychosis.



We may dismiss the latter view at once. It can readily be shown that the idea of the physical arises simultaneously with the idea of the psychical. These ideas arose together historically and they arise together in the development of the individual. Each gets its meaning in relation to the other. For this reason it is an historical fallacy to read back the meaning of the physical into a pre-psychical stage. Whatever existed before mind appeared, it cannot be what now we call matter, for our notion of what matter is has come entirely from its relation to mind. Whatever preceded the appearance of mind, therefore, is no more adequately described as physical than as psychical.



This theory of parallelism, if it is to remain parallelism at all, reduces, then, to the theory of complete parallelism. Let us turn to the latter view.

The theory of complete parallelism maintains that the physical and the psychical are two orders of reality which exist side by side without ever coming into any causal relation with one another. They constitute a dualism which runs throughout the universe, a chasm which science acknowledges she is powerless to bridge. But such a fundamental dualism in reality is a sign of false method in our knowledge. It is multiplying existences needlessly to suppose that there are two realms instead of one. Physical science is quite right in pushing so-called psychical energy over the edge of the universe. There is no need for postulating a second mode of energy which is called

psychical alongside of what we call physical energy. For, according to all scientific principles, it is quite superfluous; it accomplishes nothing that can be measured by scientific apparatus; it is inert and useless. It is a mere phantom which a persistent metaphysical superstition conjures up to mock at the supposed materialism of science. Yet even HUXLEY retains a sorry place for the psychical in this sense as a sort of epiphenomenon, like the bell on a clock or the whistle on a steamboat. Whatever truth the theory of psycho-physical parallelism may contain, it cannot lie in the conception of an ontological dualism of mind and matter.

What, then, is the true relation of the psychical and the physical? It is this. The psychical and the physical are related as function and structure are related in biology. The biologist does not hypostasize function and make a separate form of energy out of it, which then is supposed to act causally upon structure. Some biologists *have* attempted to conceive of the function as in some sense preceding the organ, of function as preceding structure. But this notion has been called, what it certainly must remain when stated in this form, the biological paradox. Its paradoxical nature really arises from a false statement of the problem. It is as false to conceive of function as preceding structure as it is to conceive of structure as preceding function. A truer statement would be that the function is the meaning or significance of the structure. By the function of an organ is meant its characteristic activity or behaviour. The function of an organ is the meaning of that organ as expressed in its activity. All genetic classifications in science are classifications based on differences of function. If I want to understand the meaning of any structure I ask how it functions. Function in biology is another word for meaning or significance.

It is in this way that the psychical is related to the physical. Matter, so to speak, is the structure, of which mind is the function, and the meaning or significance of matter comes out only in its activity, only as it functions. The psychical is not another form of energy existing alongside of or in addition to

the various forms of physical energy, and coming in either before or alongside of or subsequent to the operation of this physical energy. The psychical is the meaning of the operation of the forces in the material world.

This is the element of truth in all doctrines of parallelism, that existence always has meaning and meaning always refers to existence, that structure reveals its significance in function and function is but another name for the significance of structure—and this view is as far from materialism as it is from the opposite error of subjective idealism.

We have said that the ideas of the physical and the psychical in the sense of existence and meaning emerge together in experience. But not all our experience is characterized by a clear distinction of these two. There was a time both in the experience of the race and in individual development when these were only vaguely held apart.



In other words, the evolution of the distinction of fact and meaning, or existence and significance, has been by slow degrees, and we say that a consciousness is of a relatively low or high type according to the clearness with which this distinction is made. There is something in the experience of the savage and of the child which corresponds to what the philosopher or the scientist calls the *fact* and the *meaning* of the fact. More than this, there is in the experience of every conscious being, however low in the scale of life, something which corresponds to this same distinction. Wherever there is consciousness there is this distinction between the psychical and the physical in this sense of function and structure, or meaning and the fact of which it is the meaning; there is a distinction between something taken as actual (as fact or existence) and something taken as ideal (as meaning or significance).

With this point of view in mind, let us pass now to the

main subject, which is a statement of the conditions and stages in organic evolution. The standpoint of the psychological theory of organic evolution implies, we have seen, three things: (1) evolution, (2) that the psychical is not a form of energy, but that it is a function, and (3) that wherever we have consciousness we have at least in rudimentary form the distinction between the physical as fact and the psychical as the meaning of the fact. The bearing of this on evolution may be summed up as follows: The whole universe may be viewed from the standpoint of structure or from the standpoint of function; that is, it may be viewed as fact or as meaning. Hence the evolution of the universe may be stated in terms of function as well as in terms of structure, in terms of meaning or significance as well as in terms of fact of existence, in terms of psychology as well as in terms of physical science. That is, again, evolution admits of a teleological as well as of a mechanical statement. The mechanical statement of evolution has been worked out by such writers as DARWIN and SPENCER. It is the purpose here to show some of the implications of the teleological or psychological statement of the evolutionary process.<sup>1</sup> The discussion, as has been said, will fall into two main divisions: a consideration (1) of the evolutionary conditions of the emergence of consciousness, and (2) some of the probable stages in the evolution of consciousness.

That consciousness is coextensive with life will not seem incredible if we rid ourselves of the notion that all consciousness is of the human type and if we substitute the teleological for the ontological distinction between the physical and the psychical. All that is claimed here is that in the lower types of consciousness there is *some* holding apart of fact and meaning, *some* projection of ends and the correlative means for the attaining of those ends.

If the evolution of consciousness means anything at all it means that complex forms have evolved from simpler forms of

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<sup>1</sup> We limit ourselves here to organic evolution, i. e., to the evolution of organisms.

consciousness. We cannot get at the nature of these simpler types of consciousness directly. But we can reconstruct the evolution of the primitive consciousness from a study of the evolution of organic structure and from a study of the conscious acts of the living organisms about us.

The theory of most biologists is that the characteristic behaviour of organisms began as purely mechanical activities in the presence of stimuli, among which certain useful reactions have been preserved by natural selection, consciousness appearing at some comparatively late period in the evolution of organic structure. A few writers, however, have opposed this view. Its ablest critic, perhaps, is the late Professor COPE, in his "Origin of the Fittest" (1887) and his "Primary Factors of Organic Evolution" (1895). His view is that the primitive cell was the conscious cell, and that consciousness is coextensive with all progressive evolution of organic structure, i. e., with all "anagenesis" as opposed to "catagenesis." All organic structure, he holds, has been built up in the first instance with the accompaniment of consciousness. The impregnable argument of his theory is based on the fact that in all cases where we have the opportunity of observing the origin and growth of the reactions of organisms we find that they have to be learned, and that they become automatic only after a more or less prolonged period of conscious education.<sup>1</sup>

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<sup>1</sup> The metaphysical setting of Professor COPE's theory, as he states it in the works above mentioned, is objectionable. In two important points his statement is open to criticism, (1) in his statement that consciousness is an attribute of matter, and (2) in his conception that consciousness is an additional factor in evolution.

To speak of the latter point first. If by factors of evolution is meant simply observed uniformities in growth processes, the law of the emergence of consciousness under certain conditions of organic growth may surely be placed alongside of the laws of natural selection, use-inheritance, sexual selection, etc. But it is one thing to speak of a law of consciousness being a factor, and quite another thing to speak of consciousness itself as a factor of evolution. Moreover, Professor COPE does not adhere to this meaning of factors of evolution, but falls into the error of confusing factors in the sense of observed uniformities with factors in the sense of the realities which evolve. In other words, he views factors as efficient causes.

He contrasts his own theory with that of Mr. HUXLEY who maintains that

It must be noted that this theory makes no dogmatic assertions as to the exact distribution of consciousness in the organic realm. All evolution is not progressive. There is catagenesis as well as anagenesis, degeneration as well as generation. It is conceivable that there are degenerate forms in which consciousness seldom or never appears because the conditions of consciousness are no longer fulfilled. The theory holds simply that consciousness is always present at the initiation of new forms of activity on the part of organisms.

Various criteria have been advanced for the presence of consciousness in the reactions of organisms. The most common and popular criterion is the purposefulness of the conscious act. If an animal, or even a single organ, reacts as a man would do under the same circumstances, the act is regarded as conscious. The application of this criterion has led certain writers to include instincts and reflexes among conscious acts, and con-

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the consciousness of the brute is related to the mechanism of its body as a collateral product of its working, and is as "completely without any power of modifying that working as the steam-whistle which accompanies the work of the locomotive-engine is without influence on its machinery." The volition of the brute, if it has any, he says, "is an emotion indicative of physical changes, not the cause of such changes." Professor COPE, on the other hand, in his doctrine of archaesthetism, maintains "that consciousness as well as life preceded organism, and has been the *primum mobile* in the creation of organic structure." "I think it possible to show," he says, "that the true definition of life is, energy directed by sensibility, or by a mechanism which has originated under the direction of sensibility. If this is true, the two statements that life has preceded organism, and that consciousness has preceded organism, are co-equal expressions." (Primary Factors of Organic Evolution, p. 513).

Now neither HUXLEY nor COPE, it seems to me, has the true conception of the relation of consciousness to evolution. Consciousness is neither-effect nor cause. The psychical is not a form of energy at all. Consciousness is a function, not a thing, not an entity. Consciousness rather expresses the meaning of evolution when it is progressive. Consciousness *is* evolution in its constructive or anagenetic phase. Consciousness is the growing-point of evolution.

In what has been said, Professor COPE's second point, that consciousness is an attribute of matter or a certain behaviour of matter, as he also calls it, has implicitly been met. He evidently does not mean here that consciousness is meaning or significance, though the terms "attribute" and "behaviour" might be interpreted in that sense. What he means must be something coherent with his doctrine of archaesthetism which makes consciousness a factor in the sense of an efficient cause in evolution, and this conception certainly is indefensible.



consciousness has been ascribed even to the spinal cord because many of its functions are purposeful. But, as Professor LOEB has pointed out, there is evidence of purposeful response even in the tropisms of plants and, in his opinion, we are equally warranted on this principle in ascribing consciousness to machines and even to molecules and atoms. Evidently this criterion does not help us forward any, since it is no answer to the question as to the limits of consciousness to reply that all processes are conscious, including the chemical and physical relations of atoms and molecules. This at best simply shifts the problem back a step, since if all natural processes are conscious we still have to ask what are the limits of that peculiar form of consciousness which marks off the rational from the instinctive act. If by purposiveness is meant evident adaptation of means to ends, then purposiveness cannot be an adequate criterion for the presence of consciousness, since we find evidence of such adaptation throughout nature, as well in the inorganic and unconscious as in the organic and conscious sphere. Attention is called to this principle as a criterion of consciousness because it is a good illustration of the uncritical popular attitude toward the problem, which has found its way even into such works as that of ALFRED BINET in his study of "The Psychic Life of Micro-organisms," where the criterion used is choice or power on the part of an organism to discriminate and make a selection.

A more critical and scientific attempt to determine the criterion of consciousness is found in Professor LOEB's doctrine of "associative memory." By "associative memory" he means "that mechanism by which a stimulus brings about not only the effects which its nature and the specific structure of the irritable organ call for, but by which it brings about also the effects of other stimuli which formerly acted upon the organism almost or quite simultaneously with the stimulus in question."<sup>1</sup> Consciousness goes out with "associative memory" in sleep, in anaesthesia, in the faint, in coma due to poisons, etc. Hence "associative memory" is essential to consciousness. Conscious

<sup>1</sup> Comparative Brain Physiology and Comparative Psychology (1900), p. 12.

phenomena are phenomena which are determined by "associative memory," and an animal possesses "associative memory" if it can be trained, if it can learn by experience. Such is the argument. BETHE holds a similar view when he says that an animal "that learns nothing, that always reacts in the same way upon the same stimulus, possesses no consciousness." This doctrine may be called the theory of pre-requisite development of the nervous system. In applying this criterion Professor LOEB fails to find consciousness in such types as Infusoria, Coelenterates, and Worms, and doubts its existence in many higher forms. He is not sure as to Mollusks and Insects. He grants consciousness to Bees, Wasps, Spiders, certain Crabs and Cephalopods, but denies it to the common frog (*Rana esculenta*), though he finds it in the tree-frog. He is quite certain of the presence of consciousness only in many of the higher vertebrates. His researches upon the plant and animal tropisms leads him to think that wherever organic reactions are explicable by mechanical tropisms all reference to consciousness is excluded. "Associative memory" comes in only when tropisms fail to explain the phenomena of adaptation. Hence consciousness appears abruptly in the course of a purely mechanical evolution.

That there is an important element of truth in the conception that the ability to learn by experience is a mark of consciousness, we shall see later. The error in Professor LOEB's view consists in identifying all consciousness with that particular type of highly organized consciousness which commonly goes by the name of "associative memory." This might be a good criterion for testing the amount or degree of mammalian consciousness, but it is entirely too restricted a standard to apply to the whole animal kingdom, not to speak of the plant kingdom.

Another theory of the criterion for the presence of consciousness stands midway between the extreme views just mentioned, and is represented by such writers as SPENCER, MORGAN, ROMANES, EIMER, and CARUS. MORGAN, for example, declines to say just where consciousness begins in the evolutionary

scale, but holds that at some point or other it evolves out of unconscious or pre-conscious inorganic nature. He says, it is true, that what we call consciousness has developed from something more simple than consciousness, but of the same order of existence—"germinal states" of consciousness, as he calls them. But this must mean one of two things: either these "germinal states" are forms of consciousness, or they are not. There is no realm between the unconscious and the conscious answering to "germinal states." To posit such a realm and call it "infra-consciousness" is simply to create a problem out of words.

The other writers mentioned also hold in one form or another that consciousness appears at some point subsequent to the appearance of life upon the earth, but none of them say just where that point is to be found, and they all differ in their attribution of consciousness to certain doubtful types.

ROMANES' doctrine of the criterion of consciousness, in some of his statements, comes back to the criterion of purposiveness, though he recognizes and attempts to obviate the difficulties which that theory presents. The positive value of his criterion comes out when he states it as the ability to learn by experience. Stated in this way, his criterion of consciousness asks, "Does the organism learn to make new adjustments or to modify old ones in accordance with the results of its own individual experience?"<sup>1</sup> Purposiveness taken in itself, in other words, is not a sufficient criterion of consciousness. It is that purposiveness which is shown under conditions of organic tension that is conscious, purposiveness which involves the ability to choose this rather than that method of adaptation or adjustment. Purposiveness means simply adaptation of means to ends. *Consciousness means the ability to vary the use of means in the attainment of an end.* The former *may* be quite automatic. The latter alone *must* be conscious. ROMANES, of all these writers, comes the nearest to an adequate statement of the condition and criterion of consciousness.

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<sup>1</sup> Animal Intelligence, p. 4.

Developing this suggestion of ROMANES, we may say that the condition of consciousness is found in organic tension and the criterion of consciousness lies in the ability to vary the use of means in the attainment of an end. Experience may be viewed as an ongoing activity. When the process of coordination or adaptation of that activity is hindered in any way, consciousness supervenes as the process of removing the obstacle to free unimpeded adjustment. This wrestling with the difficulty as with an opponent, this endeavor to surmount the obstacle, this attempt to solve the problem which the difficulty presents, gives rise to a state of resistance or tension. Stated psychologically, this is attention. Attention is the mental aspect or name for organic adaptation, and is developed at the point where new habits are being acquired or where old habits are being modified in accommodation to some new situation. The conscious act is the relatively novel act on the part of the organism, the act which expresses the variant as opposed to the constant factors in its growth. Consciousness expresses the mobility of function as habit expresses the stability of structure. Consciousness, as Professor BALDWIN says, "is the new thing in nature—the thing by which organisms show in all cases their latest and finest adjustments. And the central fact of consciousness, its prime instrument, its selective agent, its seizing, grasping, relating, assimilating, apperceiving—in short, its accomodating element and process—is attention." "Whenever there is accomdation—the breaking up of habit, the effort to learn, the acquirement of new movements and coordinations of movement—there consciousness is present, and present in vivid and heightened form according as the habit fought against is fixed, and the road to the new acquisition is an uphill road. The things most new, difficult, imperfect, hard to effect, these dwell in the very focus of . . . attention."<sup>1</sup>

Consciousness, then, is born in friction, in the stress and

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<sup>1</sup> Mental Development in the Child and the Race, 168, 233.

strain of adjustment and readjustment.<sup>1</sup> Consciousness occurs wherever new experience is being acquired. All organic structure has been built up in and through consciousness. Consciousness always develops at the point at which the organism is adjusting itself to its environment or at which its various organs are becoming adjusted to one another within the organism. Hence consciousness is a moving or shifting area of tension gyrating from point to point according to the needs of the adjustment. The process of consciousness consists in the interaction of old and new habits until a new coordination arises which solves the problem and adapts the organism in the new situation. Consciousness arises in tension, but tends always to the restoration of the organic equilibrium. It always points to something beyond itself, to the new coordination, the new unified experience, the new act. The law is, that attention is developed at or in the point of difficult adjustment. Attention always goes to the weakest point, since it is always there that the readjustment must take place. Soon a new habit is built up at the weak point and then attention is directed elsewhere.

The nervous system may be viewed as an equating mechanism which serves to keep up the tension which is the condition of consciousness and to restore the equilibrium when experience takes the form of habit or automatic action. It is a special organ of control which serves to mediate between the organism and its environment by means of the sense organs and muscles. The adjustment between the environment and the organism as a whole is not the entire problem of adaption, however. There is also a constant mutual adjustment of organs within the organism. We may say that there is all the time going on a competition among the organs of the body each for complete domination of the entire organism. The whole body would be an eye or an ear or a nose, or a leg, or a hand, or a mouth. This tendency is seen in its extreme form in halluci-

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<sup>1</sup> For statements of the dynamic or equilibrium theory of consciousness, cf. DEWEY, *Monist*, Apr. 1898, 335 f; CARUS, *Soul of Man*, 194 f; HERRICK, *Journ. of Compar. Neurol.*, VI, 13 f; VII, 156, 160; VIII, 21 f.

nations, fixed ideas, and motor types, where one sense seems to carry everything before it or where one type of imagery comes to predominate, as in the so-called visuels, audiles, and moteurs. In the normal organism this competition results in a balance or, where there is call for the successive action of different functions, there will be set up a rhythmic alternation of the focus of attention from one to another of these centres of adaptation.

The conception is not, let it be noticed, that consciousness is the invariable accompaniment of all motion or movement, but that consciousness is the accompaniment or product of *relative tension*<sup>1</sup> in adaptation—*relative* tension, because the resistance which will be sufficient to produce consciousness under one set of circumstances will not be sufficient under another set of circumstances. If I am living with the roar of Niagara in my ears, the sound of the rippling brook will elicit no consciousness. But if I am strolling through the silent forest, this sound will attract my attention at once. Stated generally, tension is the condition of consciousness. What quality and quantity of tension will be required, will depend upon the situation.

Now, in the lowest organisms these conditions of tension must, of course, be very simple and the range of alternative means which can be utilized in the attaining of an end must be exceedingly limited. Contrast the problems which present themselves to the coral polyp with the problems that are involved in the adjustment of a mammal in its environment. The environment of the former is relatively homogeneous; the environment of the latter is constantly shifting, not alone by reason of an inherent evolution of the environment, but also by reason of the constant change of scene which is brought about by the voluntary movements of the animal itself. Or contrast the hunger of an oyster with the hunger of a man, and the simplicity of the means employed to satisfy this craving in the one case with the complexity of the means used in the other.

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<sup>1</sup> "Or relative equilibrium," which is the same thing (cf. HERRICK, Journ. of Compar. Neurol., VII, 155).

A thousand complicated economic and social relations enter into the spreading of the feast to which the civilized man sits down at every meal, while the hunger of the bivalve must, for the most part, await the food that chance throws in its way; there is comparatively little use even of approximate, not to speak of remote, means to achieve this end.

By the primitive consciousness, things, objects, situations, are taken in their immediacy. It is only in a highly developed consciousness that one thing comes clearly to stand for another thing, or that memory images and constructive ideas split apart the inchoate present into a definitely recognized past and future. It is because of this relative immediacy of the animal consciousness that men are loath to credit him with the ability to form judgments. The distinction of substantive and adjective, of fact and meaning, of the given and the problematic, can arise only where the knife-edge of the present has expanded so as to admit within it the distinction of past and future mediated by memory and imagination. These certainly are not found in the animal consciousness as they are found in man. But though they are not found there clearly and definitely, may they not be there vaguely? May they not be there sufficiently for the purpose in view—namely, the adaptation of the organism in the given situation? We must not fall into the historical fallacy of reading human traits back into the animal consciousness. But, on the other hand, is there not a counter danger, that in the attempt to avoid this error we fail to give the lower animals their due? It is a query worth some serious consideration.

Many writers deny that animals have any power of projecting purposes of ends, holding that in their case the action flows directly from the given conditions without any consciousness on the part of the animal of those purposes or ends. Yet these same writers will admit that animals probably feel, experience pleasure and pain. But why should the feeling of pain or pleasure ever arise if it did not serve some useful purpose for the protection and survival of the organism? And of what service would pain be as a monitor unless the animal could respond by some perception of the situation? Bare or pure feeling of pain,

if such a mental state is conceivable at all, would be of no service unless or until it stimulated some adaptation on the part of the organism. And when the latter process takes place we have all the essentials of the cognitive process, involving the projection of purposes or ends. Of course, among lower orders of intelligence these ends will be projected only in a vague and relatively uncontrolled way, and it is for that reason that we characterize such a consciousness as of the effective or impulsive as contrasted with the reflective or rational type.

Furthermore, such a low type of consciousness is not to be interpreted in terms of our individualistic selfhood. The consciousness of an oyster is the focal or tensional area in a wider field of experience, like all consciousness; but it is vaguely, not definitely, focal. It is the cognitive differentiation of the human consciousness which makes possible the individualism of human self consciousness. Just as the human consciousness of individuality emerged by slow degrees out of a sort of racial or tribal consciousness, so the higher forms of animal consciousness must have evolved by slow degrees out of that vague psychical matrix which expressed the tensional stress of some life problem of the species rather than any specific crisis in the life of an individual. Consciousness here, as everywhere, was the shifting focus of a wider sphere of adaptation, but it was focal, as yet, not for the individual organism as such, but rather for the species or clan or group or animal community of which what we should, from our point of view, call the individual organism, formed an integral part. This view is born out by the evident relation of the various instincts of animals to the life of the species.

Experience probably begins, then, in the form of vague flashes of feeling (or what is predominantly feeling) which come sporadically according to the exigencies of the life history of the form.<sup>1</sup> Consciousness becomes progressively organized in connection with the crises and emergencies of life; not continuously from the first, but in spots or patches or streaks. Its

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<sup>1</sup> Cf. STANLEY, *Evolutionary Psychology of Feeling*, p. 13.



growth is not symmetrical, but experience is built up at the points which happen to be crucial. Whether this or that individual organism in the species or group will be conscious, will depend upon whether or to what extent it stands in the focus of the organic tension. The first flash of consciousness in the lowest type of organism may well have been the last for that individual organism. And in great groups of organic forms where there is little evolutionary advance the conditions of consciousness for many individuals may never be fulfilled. As to this we can only conjecture, except as we are able to interpret the life problems of the lowest and the highest forms in terms of a common process.

The primitive consciousness, then, was an effort consciousness, which at first, it may be, was predominantly painful. As Professor COPE says, "The preliminary to any animal movement which is not automatic, is an effort. And as no adaptive movement is automatic the first time it is performed, we may regard effort as the immediate source of all movement. Now, effort is a conscious state, and is a sense of resistance to be overcome. When an act is performed without effort, resistance has been overcome, and the mechanism necessary for the performance of the act has been completed. The stage of automatism has been reached. But at the inception of a new movement resistance is necessarily experienced."<sup>1</sup> All progressive evolution, you may say, has its origin in the "strenuous life."

The situation which will call forth consciousness in the lower animal is altogether determined by its needs either as an individual or as representing the species. Consciousness develops in connection with the crucial problems which it has to solve in order to maintain its existence, in order to survive. These vital needs and crucial problems will be connected with such conditions as the changes in the seasons; the periodicity of the appearance of vegetable food; the irregular production of animal food; the struggle for existence between animals themselves; the separation of feeding and breeding areas; glacial

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<sup>1</sup> Primary Factors of Organic Evolution, p. 498.

invasions, floods and drought; earthquakes, volcanoes and landslides; the submersion and elevation of continents and islands; the drying up of inland seas; changes of ocean and air currents; in short, any catastrophic or cataclysmic changes in nature. And to such abrupt general changes we must add all sorts of chemical agents, physical strains and contacts, mechanical hindrances or helps to growth, changes in light, moisture, temperature, etc. These are only a few of the many conditions that might be named which would give rise to the necessity of new adaptations on the part of organisms. It would be interesting to know in detail the steps by which certain land forms returned to an aquatic life, certain mammals took to burrowing in the earth and others to an arboreal life. What led to the divergence of the birds and reptiles from a common stock? Why did the birds develop nidification and incubation and the mammals the placenta? How did animals first come to hibernate? What stress of conditions in the struggle for life led to the keen development of the sense of smell in the deer or the hound? Under the stress of what economic problems was fire first discovered or huts first built or clothing first worn?

It must be remembered that these problems were solved one by one in the evolution of consciousness. They did not come to the primitive consciousness in their ensemble as they appear to us. The chief objection that has been raised to the work of the recent experimental school of comparative psychologists has been that the artificial conditions of the experiments interfere with the natural instincts and proclivities of the animal. The conditions of the experiments do not approximate the conditions to which the animal is subjected in the state of nature. Hence the conclusions based on observation of animals under such conditions are apt to be distorted. An animal can only be expected to exhibit what rationality it possesses when the problem to be solved lies in the line of its inherent abilities. It is not remarkable that an animal when placed in a situation which is almost wholly different from any of the typical situations into which it is liable to be thrown in its natural state, should respond to that situation quite blindly and vaguely. The

results of such experiment show how difficult it is to devise problems which shall be at once congruous with the life of the lower animal and at the same time definite enough to prove of any scientific value.

Summing up the main points we have covered so far, we have seen that the evolution of consciousness has been conditioned by factors of organic tension arising in connection with the attempt to solve crucial life problems, the criterion for the presence of consciousness in an organism being the possession of ability to vary the means employed in the adaptation, the ability to use this rather than that existent means to get a desired end.

We come now to the second main consideration, as to the probable stages in the evolution of consciousness. The first question to be asked here, I suppose, would be as to the vegetable world. Are plants conscious? We have criticized the view that denies all consciousness to the lower organisms. But we need not fall into the opposite error of supposing that the organism is necessarily always conscious. It is evident that many types which have deviated from the onward movement of evolutionary growth or have distinctly retrograded, will no longer present the conditions of struggle or tension requisite for the presence of consciousness. HERBERT SPENCER has generalized the truth that motion, that activity, always follows the line of least resistance. Now the line of least resistance is the line or path of habit, of automatic action. It is for this reason that motion is rhythmic. The mechanized act is necessarily rhythmical, since any variant element would interfere with the smoothness of the coordination and thus call forth consciousness. Where an organism becomes adapted to a relatively fixed environment with little or no occasion for variation in the means necessary for the adaptation, consciousness will subside if not vanish altogether. The process of adjustment becoming automatic, attention, or consciousness, is no longer needed and accordingly disappears. In this way among the lowest organisms all mind may have passed into the reflex stage after adapting the species to its environment,

From the standpoint of the ongoing evolutionary movement such adapted organisms are degenerate forms. In Professor COPE's words, we have "catagenesis" in place of "anagenesis." Such, Professor COPE thinks, is the history of the entire vegetable kingdom. "From their ability to manufacture protoplasm from inorganic substances, plants do not need to move about in search for food, so that they require no consciousness of conditions to guide their movements. They become fixed, and their entire organization becomes monopolized by the functions of nutrition and reproduction. Movements rarely occur, and when present . . . are mostly rhythmic or rotary, and very seldom exhibit the quality of impromptu design."<sup>1</sup> Plants may thus be viewed, he thinks, as degenerate descendants of Protozoan animal ancestors. There is every reason to believe that the ancestors of the present higher types of plants were more animal-like than they. Along with the degeneration of certain of these Protozoan types, in which, instead of being free-moving they become sessile, there has gone the mechanization of the process of adjustment to the environment, with the consequent subsiding of consciousness. Consciousness early abandoned the vegetable line, or at least is found there only in its most rudimental form.

This is why the evolution of consciousness has taken place mainly along the animal line. "The animal," says Professor COPE, "may have originated in this wise. Some individual protists, perhaps accidentally, devoured some of their fellows. The easy nutrition which ensued was probably pleasurable, and once enjoyed was repeated, and soon became a habit. The excess of energy thus saved from the laborious process of making protoplasm was available as the vehicle of consciousness and motion. From that day to this, consciousness has abandoned few if any members of the animal kingdom. . . There is abundant evidence to show that the permanent and the successful forms have ever been those in which motion and sensibility have been preserved, and most highly developed." "In

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<sup>1</sup> Ibid, p. 509.

accordance with this view the automatic 'involuntary' movements of the heart, intestines, reproductive systems, etc., were organized in primitive and simple animals in successive states of consciousness, which stimulated 'voluntary' movements, which ultimately became rhythmic; whose results varied with the machinery already existing and the material at hand for use. It is not inconceivable that circulation may have been established by the suffering produced by an overloaded stomach demanding distribution of its contents. The structure of the Infusoria offers the conditions of such a process. A want of propulsion in a stomach or body-sack occupied with its own functions would lead to a painful clogging of the flow of its products, and the 'voluntary' contractility of the body or tube-wall being thus stimulated, would at some point originate the pulsation necessary to relieve the tension. Thus might have originated the 'contractile vesicle' or contractile tube of some Protozoa; its ultimate product being the mammalian heart. So with reproduction. Perhaps an excess of assimilation in well-fed individuals of the first animals led to the discovery that self-division constituted a relief from the oppression of too great bulk. With the increasing specialization of form, this process would become necessarily localized in the body, and growth would repeat such resulting structure in descent as readily as any of the other structural peculiarities. No function of the higher animals bears the mark of conscious origin more than this one, as consciousness is still one of the conditions of its performance. While less completely 'voluntary' than muscular action, it is more dependent on stimulus for its initial movements, and does not in these display the unconscious automatism characteristic of many other functions."<sup>1</sup>

If this theory is sound, then all that HUXLEY has to say about animal automatism and all that Professor LOEB urges from the side of animal tropisms may be true (so far as the *facts* are concerned) and still not be incompatible with our theory of the evolution of consciousness. For, from this point of view, tro-

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<sup>1</sup> Ibid. p. 517.

pisms represent the mechanized background or marginal context of that focal experience which we call consciousness. Here also is the reason why the spinal soul in man is a myth, while a consciousness in the analogue of the spinal cord in the phyletic series may be a reality.<sup>1</sup> This theory also furnishes a rational distinction between intelligence and reason, concerning which there has been so much controversy among comparative psychologists. An *intelligent* act is an act which implies adaptation of means to ends; it is the purposive act. A conscious act, i. e., a *rational* act, is one which reveals the ability to vary the means in the achievement of the end. All intelligent acts have passed through the conscious phase, but have become mechanized or automatised in the form of instinctive reflexes. Each reflex and instinct represents a habit which has been built up in the phylogenetic struggle in connection with such an amount and kind of consciousness as was necessary to rally the animal for a crisis.

We have not the facts to enable us to sketch in detail the stages in the evolution of animal consciousness. An instructive outline of the probable steps, however, forms the substance of a course of lectures on comparative psychology by Professor GEORGE H. MEAD of the University of Chicago, which have not as yet been published. I will give in my own words the drift of that part of his argument which is relevant here as I recall it from his lectures to which it was once my privilege to listen.

Our general principle is that no psychical function appears except as relative to some definite end and that such an end is found in primitive forms in the reactions necessary to the preservation of the species or of the individual. And we have seen, that progressive evolution has been in and through the animal rather than the plant.

Now, Professor MEAD shows that the plant continues to play an important part in this evolution, in that the animal is

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<sup>1</sup> And here is the element of truth in the theory of partial parallelism, that while every psychosis has its neurosis, not every neurosis has its psychosis.

entirely dependent upon it for food. A large number of animals are carnivorous, it is true, but these prey upon herbivorous animals which, for their part, live entirely upon plants. One of the problems which the animal has to face, then, is the problem of nutrition in all its various forms. This problem of food will be a different one for the flesh-eating than for the plant-eating animal. This is represented in the difference in the structure of the two types. The ox has a gut which is thirty times its own length, while the tiger or lion has a gut which is only eight times its own length. This is a rough index of the amount of energy required for the digestion of the two kinds of food.

But an even greater problem was that which the herbivorous animal had to face when it passed from an aquatic to a terrestrial life. The primitive plant-animal or animal-plant was unquestionably an aquatic form. Life first appeared in unicellular organisms which floated on the surface of the primordial sea where surface stretches of water were the first habitable spots. Such an organism existed in a comparatively homogeneous environment where its food supply was constantly at hand, requiring at most the development of only very simply organs to adapt it in its environment. On the surface of the ocean there was an even distribution of light and heat, as well as of food supply, so that there was no necessity for the development of special sense organs for perceiving the distant object or of complicated organs of locomotion for reaching it. But in contrast with this, imagine what was required when the animal passed from the water to the land. Its food no longer lies about it evenly distributed in a homogeneous liquid medium. Yet such a medium is absolutely essential to the continued existence of a living cell. How shall the animal be enabled to live a terrestrial existence and yet retain a liquid medium for its growing cells? How the problem was solved is obvious in the structure of any multicellular animal. The liquid environment was transferred within the organism. The cells of the human body, for example, are as really water forms as is the diatom or the amoeba. They are embathed in lymph. The leucocyte and red blood corpuscle even retain the primitive characteristics in some re-

spects. This might rudely be schematized by saying that if you were to take all the cells of the human body and spread them over surface of the ocean they would have to spread over an expanse which would contain as much nourishment as is found in the fluids of the body.

Now wherever the plant or animal passes from the water to the land environment it must carry its fluid medium with it. The most important distinction between the unicellular and the multicellular forms is that the multicellular form in this way controls the medium which surrounds its cells, while the unicellular form moves about in a medium over which it has no control, simply picking up what food it can. The multicellular form keeps its interior fluids at an even temperature by protective coverings and a vasomotor mechanism, and restores the nutritive fluids regularly by means of the digestion of food and the respiration of air.<sup>1</sup> Animals obviously would follow plants in the passage to the land, since they are dependent upon them for food. Transition types are to be found today in the amphibians which live partly on land and partly in the water. Now as the plant puts on protective layers of cellulose to shield its growing cells from destructive changes in the environment conditions, it thereby presents a new problem to the animal. These epidermal layers which protect the plant are an obstacle to the animal's appropriation of it as food. The plant, so to speak, has erected a barrier between itself and the animal. Hence the terrestrial animal must develop in corresponding complexity in order to overcome this barrier. How this obstacle is overcome we have seen as it is roughly indicated in the specialized mechanism for digestion in the ruminant. Practically the entire energy of the ruminant with its series of stomachs (one of them a sort of bacteriological laboratory) is devoted to the breaking down of the cellulose tissue in which its nourishment lies.

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<sup>1</sup> Cf. the development of the amnion and the serolemma in the Amniotes when the proreptilia passed to a terrestrial life. The amphibia are devoid of these foetal membranes: they would have been superfluous in aquatic forms.



This same food problem may be stated in another way. The instinct of hunger, as SPENCER has pointed out, lies at the basis of the development of intelligence, as that of sex (in the broad sense) lies at the basis of social organization. The nutritive function as it develops implies three things wherever the problem becomes at all complex. It involves, first, the recognition of the distant food object, secondly, movement toward it, and thirdly, the oral or manual manipulation of it when reached. With the appearance of the multicellular form the growth of definite organs for the perception and securing of food not immediately at hand becomes a prime necessity. The multicellular animal probably originated as a sessile form on elevated areas of the ocean bottom where an abundance of food obviated the necessity that each cell should lead an independent existence in the struggle for life. But as the growth of the sessile form exceeded the resources of the immediate environment to supply nourishment for the increasing number of cells, it became necessary for free moving forms again to develop. Slow moving spherical forms like the Medusa, or Jelly-fish, probably represent the first stages. More rapidly moving forms would tend to take on an elongated shape, bilaterally symmetrical, and later, as definite organs for apprehending and dealing with the distant object develop, we get the appearance of distinct head and tail ends in the animal. As has been seen, there is no necessity for the plant to develop special sense organs or organs of locomotion, since the sources of its food are found in the soil and air which immediately surround it. But the animal must develop such organs or perish. And the development of these organs means the development of intelligence.

The recognition of the distant object involves the psychogenesis of the various senses, most of which finally come to be massed in the head. The first sense imagery to develop, naturally, would be the tactile imagery, because it was first and most closely associated with all the vital processes of the food function. The first tactile imagery was doubtless that developed in connection with the ingestion of the food object and, from the standpoint of the food process, all the other senses and

functions may be regarded as developed ultimately for the sake of this process of manipulation and ingestion. Taste, smell, the static sense, hearing and sight, can all be shown to have been developed for the sake of perceiving the distant food or sex object. And locomotion is instrumental to the same end. The leg was developed for the sake of the jaw, not the jaw for the sake of the leg. All these successive developments of organs are more or less plainly designed to mediate the act of bringing the distant object to the mouth—or, at least, to mediate the manipulation of it in such a way as, sooner or later, to bring about gratification of some sort.

Thus we have seen how in and through the attempt to solve great life problems the evolving animal form has gradually extended the sphere of its activity by means of the development of organs both sensory and motor for relating it in a larger environment. As LOTZE has pointed out, when a person takes a stick in his hand to feel his way in the dark he thereby enlarges his immediate tactual or contact environment by the length of the stick itself, or, looking at it from the other side, he thereby enlarges his own personality, his own organism. So with the telescope or microscope: they are but extensions of the eye. The steam-hammer and sewing-machine and reaper are extensions of the hand. The locomotive, bicycle, ship, aerodrome are extensions of the leg or wing. It is the first great upward step in the evolution of consciousness when the animal begins to state its environment in terms of its own activity. The space and time worlds represent simply the attempt of the animal to state in the form of practically useful equations the mutual relations between the tactual, the visual and the kinaesthetic imagery.

*Vassar College.*

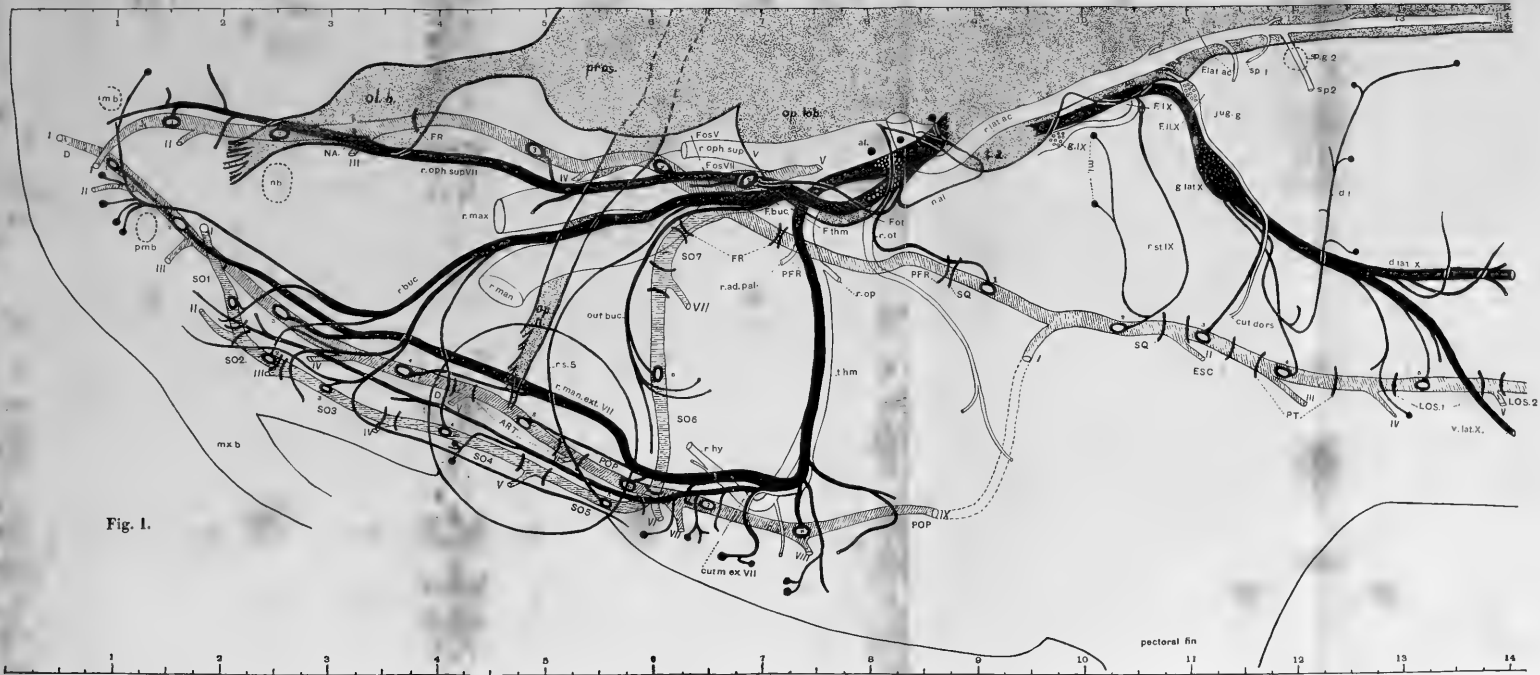


Fig. 1.



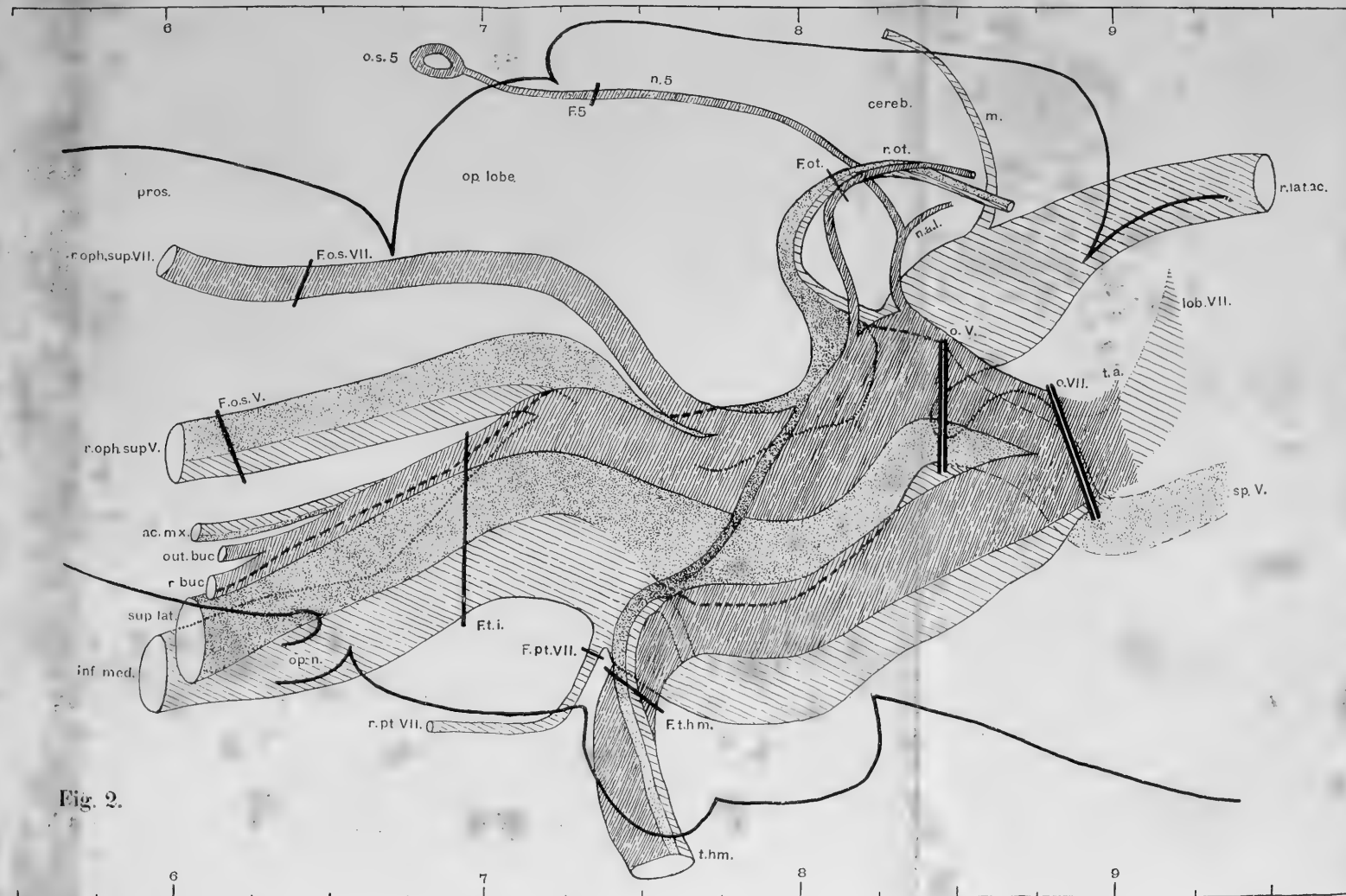
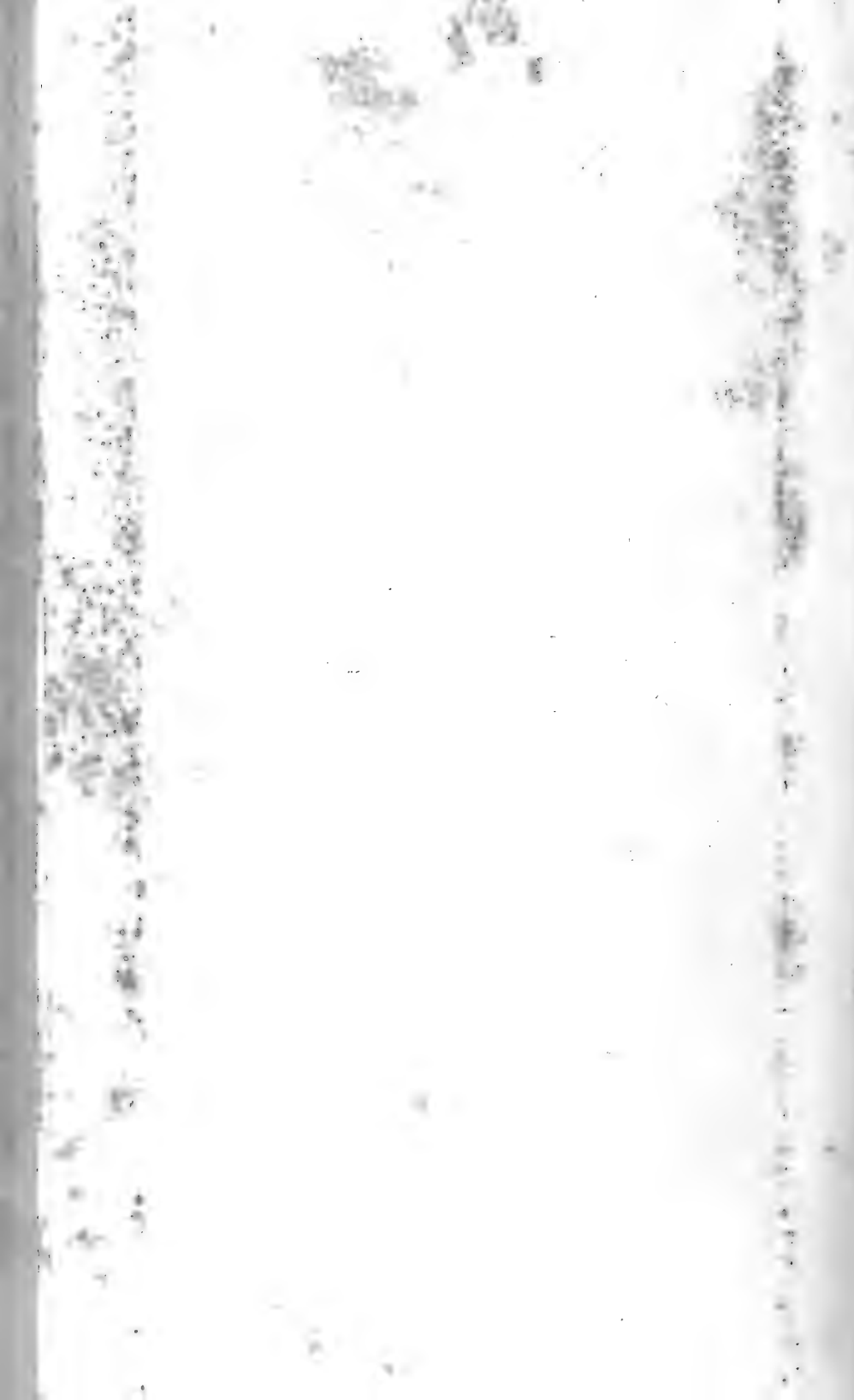


Fig. 2.



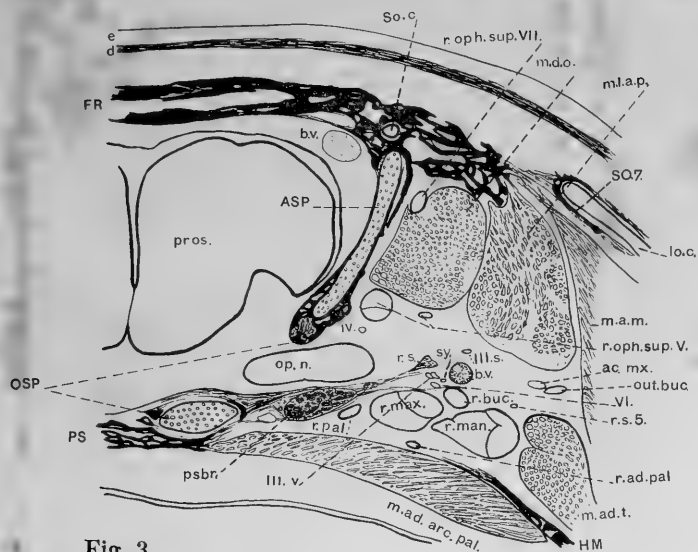


Fig. 3.

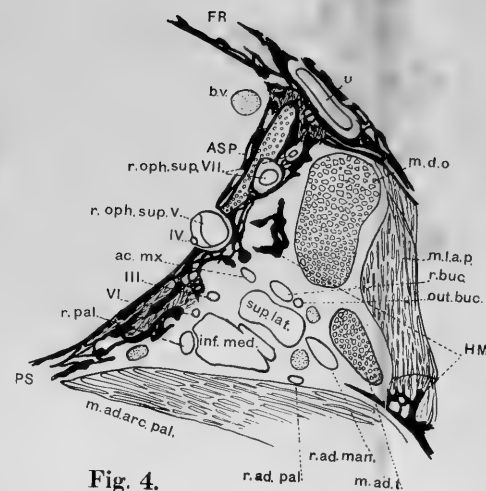


Fig. 4.

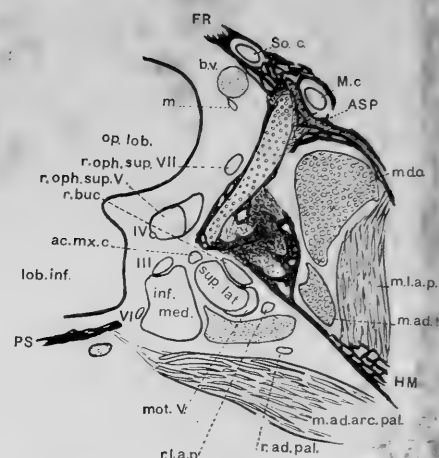


Fig. 5.

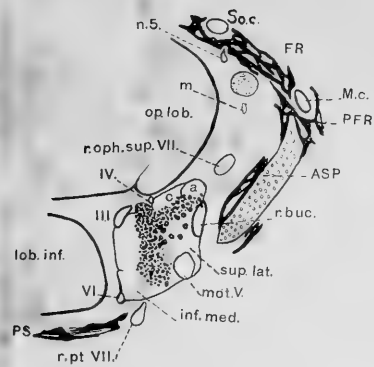


Fig. 6.

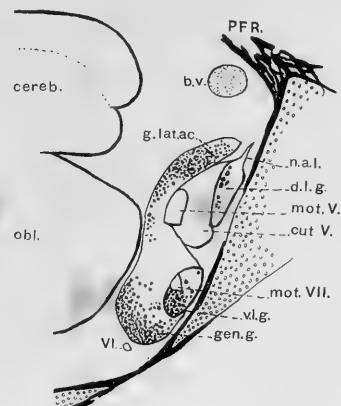


Fig. 7.

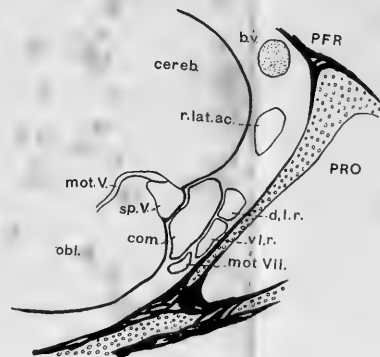


Fig. 8.

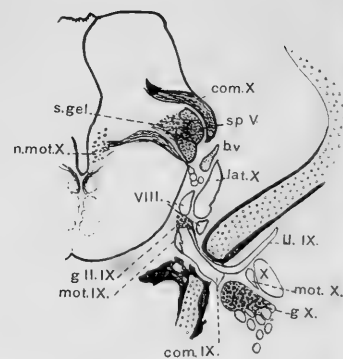


Fig. 9.





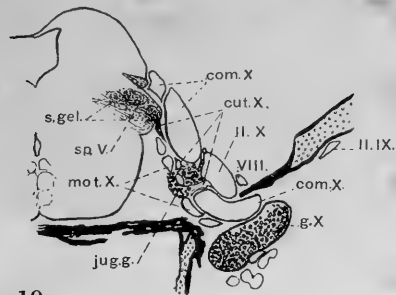


Fig. 10.

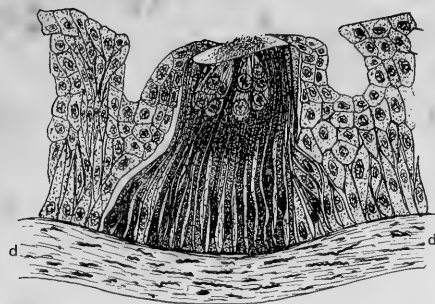


Fig. 13.

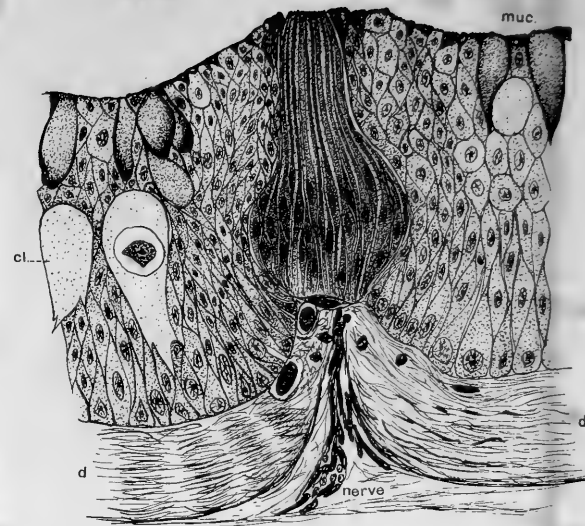


Fig. 11.

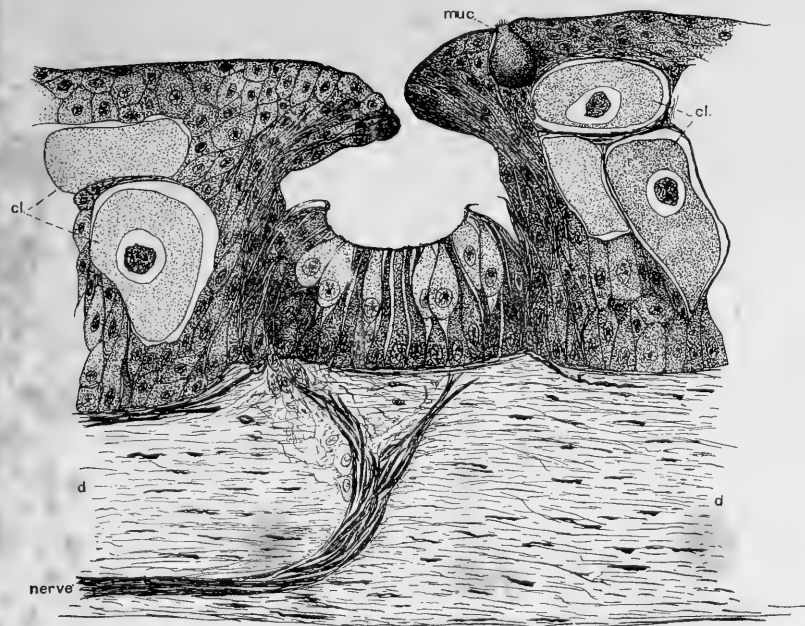


Fig. 12.

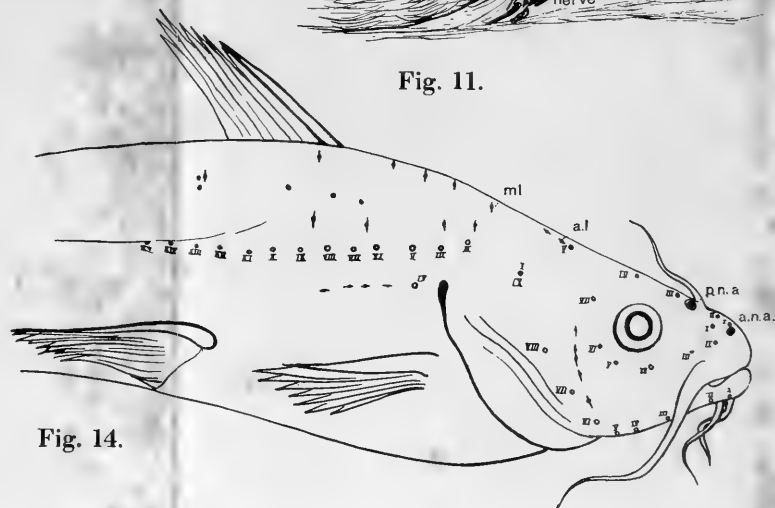


Fig. 14.



## JOURNAL OF COMPARATIVE NEUROLOGY.

ON THE MITOSIS IN THE NERVE CELLS OF THE  
CEREBELLAR CORTEX OF FOETAL CATS.<sup>1</sup>

By SHINKISHI HATAI.

*(From the Neurological Laboratory of the University of Chicago.)*<sup>1</sup>

With Plate XVIII.

- I. *Introduction.*
- II. *Materials used and technique employed for the present investigation.*
- III. *Germinal cells or "Keimzellen."*
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  - B. Germinal cells in the metaphase.
  - C. Germinal cells in the anaphase.
  - D. Germinal cells in the telophase.
- IV. *Comparison with results of other investigators.*
- V. *Morphology of the nucleolus.*
- VI. *Critique of the observations of previous authors on the nucleolus.*
- VII. *Summary.*
- VIII. *Illustrations.*

*I. Introduction.*

In the immature and growing mammalian nervous system, mitoses are very widely distributed. Mitotic changes in the cells of the central nervous system also occur in mature mammals under pathological conditions resulting from intoxication and mechanical lesions. FRIEDMAN,<sup>2</sup> MARINESCO<sup>3</sup> and TEDES-

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<sup>1</sup> This work was begun at the Biological Laboratory of the University of Cincinnati and finished in the Neurological Laboratory of the University of Chicago.

<sup>2</sup> FRIEDMAN: *Arch. f. Psychiatrie*, Bd. XIX, '88; Bd. XXI, '89.

<sup>3</sup> MARINESCO: *Semaine Med.* '94, n. 29.

CHI<sup>1</sup> have reported the former, and GOLGI<sup>2</sup> and LEVI<sup>3</sup> the latter. To determine what the value of the mitotic changes were when pathologically induced, it was desirable to gather more details as to the changes in the nucleus during normal mitosis, and to this end the present investigation was undertaken.

## II. *Materials used and technique employed for the present investigation.*

For the present investigation, foetal cats were exclusively used, the foetuses having body length (from the tip of the head to the origin of the tail) of 6.3 cm. At this stage of development they present abundant mitotic figures in almost every part of the encephalon, especially in the cerebellar cortex and the lining layer of the lateral ventricles of the hemispheres. Single sections of spinal cord of these cats showed rarely more than one or two dividing cells, and sometimes none were present. Five foetuses of the same litter were used for this investigation. As a preserving agent, GILSON's fluid, CARNOY's mixture, and RIPART and PETIT's fluid were employed in each case. The following is a formula recommended by RIPART and PETIT:<sup>4</sup>

Camphor water (dilute)	. . .	75 grams.
Distilled water	. . .	75 grams.
Crystalized acetic acid	. . .	1 gram.
Acetate of Copper	. . .	0.30 gram.
Chloride of Copper	. . .	0.39 gram.

(Osmic acid may be added to the fluid of RIPART and PETIT to increase the fixing power.)

In each case the fluid was used according to the direction

<sup>1</sup> TEDESCHI: Anatomisch-pathologische und experimentelle Untersuchungen über die Regeneration des Nervengewebes. Vor. Mitth. *Centralbl. f. Allg. Path. u. path. Anat.*, Bd. VIII ('96); also Anatomische-experimentelle Beiträge zum Studien der Regeneration des Gewebes des Centralnervensystems. *Beitr. z. path. Anat. u. z. Allg. Path.* '97, XXI.

<sup>2</sup> GOLGI: *Berliner Klin. Wochenschr.* '94, p. 325.

<sup>3</sup> LEVI: Ricerche sulla capacità proliferativa della cellula nervosa. *Rev. di patol. Nerv. e Ment.*, '96, f, 10; also Sulla cariocinesi delle cellule nervose. *Rev. di patol. nerv. e ment.*, '98, f. 3.

<sup>4</sup> This formula is given in LEE's *Microtömist's Vade Mecum*.

given by the authors. GILSON'S fluid always gave satisfactory results.

The materials preserved with the fluids mentioned, were carried through graded alcohols and embedded in paraffin in the usual way. The sections were cut three micra in thickness.

As the staining reagents, HERMANN'S saffranin and gentian violet, BIONDI-EHRLICH'S tri-color mixture, toluidin blue in aqueous saturated solution followed by erythrosin of 1% solution in 70% alcohol, and HEIDENHAIN'S iron-haematoxylin followed by either Bordeaux red or orange G in 1% solution in distilled water, were employed in each case.

In general, HEIDENHAIN'S iron-haematoxylin followed by Bordeaux red or orange G gives a very satisfactory staining of the mitotic figures. However, for the structure of the chromatic thread, for the relations of linin to the chromatin, and especially for the peculiarities of the nucleolus in active division, as well as during the resting stage, HERMANN'S or BIONDI-EHRLICH'S staining method gave more satisfactory results. The writer used also NISSL'S methylen-blue method, but the results were less satisfactory than those obtained from the fluids just mentioned. In each case, the sections should be stained slowly by long immersion in dilute solutions; otherwise, artifacts are obtained.

### *III. Germinal cells, or "Keimzellen."*

In an early stage of development, the central nervous system is formed by a long continuous tube composed of several layers of the epithelial cells derived from the ectoderm. The wall of the neural tube soon becomes thicker as a result of the proliferation of the ectodermal cells of the primitive tube. This proliferation is due to the division of the cells which lie near the lumen of the tube. These cells were called germinal cells or "Keimzellen" by HIS.<sup>1</sup>

Whether at some time in their history all the ectodermal cells which form the primitive neural tube un-

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<sup>1</sup> HIS: Die Neuroblasten und ihre Entstehung im embryonalen Mark. *Abhandl. d. Nat. Phys. Kl. d. Königl. Sächs. Gesellsch. d. Wiss.* Bd. 15, '89.

dergo mitotic division, or whether some of the cells only have this power, is not definitely known. If the latter supposition is true, then the real relations of these cells to the remaining part of the ectodermal cells must be one of the important subjects to be investigated. It has been claimed by HIS that the germinal cells are fundamentally different from the rest of the epithelial cells. This idea of HIS, however, has been opposed by many investigators (VON KÖLLIKER,<sup>1</sup> VIGNAL, SCHAPER,<sup>2</sup> etc.)

SCHAPER has reached the same conclusion as VON KÖLLIKER, urging that the germinal cells are really young proliferating forms of epithelial cells which first gave rise to indifferent cells. These latter may be further differentiated, either into nerve cells or into glia cells.

On the assumption that the germinal cells produce two kinds of tissues, either nerve cells or glia cells, the primitive form of these two kinds of cells has been named by HIS neuroblasts and spongioblasts respectively. The early differentiation of these cells will not be discussed by this paper. The observations here recorded apply exclusively to well characterized germinal cells.

The germinal cells of the cerebellar cortex of foetal cats, present a very characteristic appearance with their circular outline, and well stained chromosomes. The size of the cell-body is variable according to the phase of nuclear change which is exhibited. The measurements of the cell-bodies will be given in the descriptions of the several phases.

The various phases of the germinal cells in their development may be described advantageously in the following order:

*A. Germinal Cell in the Prophase.* In the earliest stage of this phase (Fig. 1), the germinal cells assume a nearly spherical shape. The cell-body<sup>3</sup> enlarges slightly, measuring from

<sup>1</sup> VON KÖLLIKER: Handbuch der Gewebelehre des Menschen, Bd. II, '96.

<sup>2</sup> SCHAPER, A.: Die frühesten Differenzierungsvorgänge im Centralnervensystem; Kritische Studie und Versuch einer Geschichte der Entwicklung nervösen Substanz. *Arch. f. Entwicklungsmechn. d. Organ.* Bd. V, '97.

<sup>3</sup> There occurs considerable variation of the size of the cell-body as well as nuclear area, in each phase. The present investigation applies exclusively to the cells of large size.

$4 \times 3.6$  micra to  $6.3 \times 6.3$  micra in diameter. Moreover, germinal cells contain chromosomes more deeply stained than those of the resting epithelial cells, presenting bluish red tints after HERMANN'S method.

The cell-body, as well as the nuclear membrane, is distinctly visible in the germinal cells. The chromosomes occur in great abundance and are distributed throughout the nucleus. The linin is clearly distinguishable from the rest of the other structures, while in the epithelial cell, it is extremely hard to distinguish it. The most conspicuous, as well as most important changes in this phase, are the nucleolar movements. In the inactive epithelial cell, the nucleolus appears as a compact and homogeneous structure, lying within the nucleus (Fig. 24). This simple structure, however, separates into numerous granules, owing to a solution of the linin which intimately surrounds the nucleolus in its resting stage (Fig. 24). The structural relations of these small granules in the nucleolus will be discussed later.

Following this stage just mentioned, a most remarkable change is exhibited by the chromosomes.<sup>1</sup>

As figure 2 shows, the chromatic granules enlarge considerably, and at the same time a diminution in the number of the granules takes place. The chromosomes in this stage stain more intensely than in the first case, and also the reddish color predominates over the bluish (HERMANN'S method). The cell-membrane, the nuclear membrane, and the nucleolus, are clearly visible, although in some cases, the nucleolus dissolves into numerous minute corpuscles. The linin network, in which the chromatin granules are suspended in the resting stage, becomes distinct. The centrosome lies at one side close to the nucleus.

Fig. 3 shows some very important changes of the chromatic granules. The chromatic granules, which are scattered throughout the nucleus in the former stages, now arrange them-

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<sup>1</sup> In this stage the cell-body, measures about  $9 \times 6.3$  micra to  $12.6 \times 7$  in diameter, while nucleus measures  $5.4 \times 5.7$  micra to  $11.7 \times 7$  respectively.

selves in a regular manner so as to make a continuous winding thread; this is the "spireme stage." This thread which carries the chromatic granules does not maintain the same diameter along its entire course, but is divided into numerous internodes by the larger granules which are suspended at regular intervals along the thread. The number of the small chromatic granules lying in the internodes, as well as the length of each internode, is variable. The whole number of internodes, however, seems to be always constant. In many instances, in this stage, the nucleolus, as seen in the resting state, does not appear. The cytoplasmic part of the cells stains very faintly, and is hardly visible. The thread which carries the chromatic granules is formed probably by two different substances. One of these is the linin which directly surrounds the granules, although it stains very faintly, and another substance which intimately surrounds or ensheaths the entire structure (linin and chromatic granules combined). Both of these are derived from the nucleolus. Very careful observation shows that the real chromatin substance stains an intense bluish red color, while the rest of the thread takes a bright red color after HERMANN'S method. The nucleolar substance not only covers over the spireme, but also is scattered throughout the nucleus, forming a network (Fig. 3). The centrosome lies at one pole of the oval nucleus. The spireme later accumulates at the center of the cell-body, as Figure 4 shows. In this stage, the most important change of the mitotic figure is that shown by the chromatic granules. As is shown in Fig. 3 and also is still partially visible in Fig. 4, the chromatic granules aggregate, forming larger masses of the same substance. Whether each large mass of the chromatin corresponds to each of the internodes of the thread respectively, is not clear. These chromatic masses are somewhat bean-shaped and stain an intense bluish red color. The nucleolar, as well as linin substance which forms the thread in an early spireme stage ensheaths its chromatin, as Fig. 4 shows. The gradation from spireme to that of the aggregated form of the chromatin (Fig. 6) is beautifully shown in this figure. Another important



change occurring in this stage is a disappearance of the nuclear membrane.

Fig. 5 shows the completion of the former stage, presenting sixteen large masses, one of which exhibits a dumb-bell shape. The large chromosomes thus formed by the accumulation of the smaller chromatic granules are disconnected from one another. These separate bean-shaped masses next become somewhat dumb-bell shaped; then these masses fuse together end to end, thus forming again a long continuous strand (Fig. 6). The number of the internodes composing this strand is found to be always sixteen. The connecting pieces of each dumb-bell shaped mass are frequently considerably diminished, both in length and in diameter; and very often the enlarged ends of each dumb-bell are drawn out towards the center of the circle. Thus the two neighboring ends form a V-shaped mass with the tip towards the center. This case is very well shown in Figs. 6 and 7. Still another variation of the figure which is met very often, is the intimate union of two dumb-bells. Fig. 10 is an example of this. The small letter (a) of the figure marks the chromosomes where two dumb-bells lie parallel and close together, thus giving the appearance of a single rod. This union of the two dumb-bell shaped masses into a single rod makes it difficult in some cases to count the exact number of chromosomes. In this stage the chromosomes stain most intensely. After the chromosomes combine to form a strand composed of dumb-bell shaped masses, the strand forms a ring, the constituents of which are the V-shaped bodies just described (Fig. 9). This mitotic figure forms the "equatorial plate."

Fig. 9 is a side view of the germinal cells in this stage. Besides the changes of the chromatic substance already mentioned, there are also important changes of the centrosome. Correlated with the changes in the chromatic substance is a migration of one of the central corpuscles to the opposite pole of the nucleus, but in this instance, the migration could not be followed.

From the fragmentary observations of the migration of the centrosome, the present writer believes that one of the central

corpuscles migrates toward the pole opposite to that at which it originates—this migration very probably is correlated with disappearance of the nuclear membrane—and after it reaches its final position, the centrosome divides into two corpuscles, and at the same time the original non-migrating central corpuscles also divides into two, thus forming two central corpuscles at each pole.

The next important event is the formation of the "aster." As figure 9 shows, the somewhat parallel rays formed by minute microsomes connect the two poles; that is, the centrosomes in both poles are connected with these numerous rays. These rays, or "Halbspindelfasern" of HERMANN, are quite different from the rest of the aster rays which also arise from the centrosomes and radiate outwards in all directions. The "Halbspindel" rays are stained intensely with reddish color (HERMANN'S method), while the other rays stain very faintly. Not only is this so, but the former parallel rays are composed entirely of coarser granules than compose the latter. Furthermore, the rays of the latter are directly continuous with the cytotreticulum, while the Halbspindelen rays do not show such continuation, as far as our observation went. The peculiar differences between the "Halbspindelfasern" and the rest of the archoplasm were first reported by LEVI ('98), who studied the mitosis of the nerve cells of the guinea-pig under pathological conditions following mechanical injury, and further LEVI suggested that the "Halbspindelfasern" are directly derived from the acidophile part of the resting nucleolus. Though LEVI has pointed out only the "Halbspindelfasern" as directly derived from nucleolus, the writer's specimens show that a part of the central spindle fiber also has been derived in the same way.

As was mentioned already, the chromosomes in an early spireme stage are surrounded by the nucleolar substance, and this substance, in the next stage, is transformed into parallel rays and extends toward both poles, and finally forms the "Halbspindelfasern." This can easily be followed if one compares the granules which form the spindle with those of the nucleolar sheath of the chromosomes in an early spireme stage.

Fig. 10 is a somewhat polar view of the mitotic figure in the metaphase. The continuous segmented spireme shows, in most cases, a modified dumb-bell shape as was mentioned above. Fig. 7 is a polar view of the equatorial plate drawn in optical section. This figure presents also a modified segmented spireme. Fig. 8 is a cross section of the mitotic figure passing through a plane near the middle of the equatorial plate. The continuous chromosomes were cut in such a way as to present discontinuous V-shaped bodies. The nucleolar substance which thickly surrounds the chromosomes, and also the radial arrangement of the same substance from the center toward the periphery, are distinctly visible in the space surrounded by the chromosomes. This radial arrangement of the nucleolar substance is much more clearly noticeable in Fig. 7.

*B. Germinal Cells in the Metaphase.* In this phase the chromosomes forming the equatorial plate lose their regular arrangement and lie somewhat irregularly in the equator of the cell-body (Figs. 11 and 12). Meanwhile with this change, each internode of the continuous segmented spireme splits along its long axis. This split, however, stops at the terminal enlarged bulbs; that is, both extremities of the dumb-bell remain undivided. In some cases, these terminal bulbs show deep constrictions along the middle, as can be seen in Fig. 11. Curiously enough, when each internode divides longitudinally, then new enlargements or knobs are produced, one on each side near the middle of each daughter chromosome. This is indistinctly visible in Fig. 11, but plainly shown in Fig. 13. When the chromosomes split longitudinally, the nuclear substance still surrounds the figures, except in very few cases where the nucleolar substance is only visible surrounding each daughter chromosome, but does not fill up the space newly formed by the splitting. After the splitting processes have been completed, the continuously segmented spireme rearranges itself in a manner different from the equatorial plate (Fig. 9) already mentioned; that is, the enlarged portion of the dumb-bell in Fig. 9 lies along the equator of the figure, and the knobs newly formed at the middle point of each daughter chromo-

some, form two rows on either side of the equatorial line and parallel to it. This complicated structure is clearly visible in Figs. 13, 14 and 15.

In this stage, the nucleolar substance, in most of the cases, is accumulated at the two ends of the chromatic figure, although a small quantity of the same substance is also visible surrounding each daughter chromosome (Figs. 14 and 15). Fig. 15 is a semi-diagrammatic drawing to show the real arrangement of the chromosome in this stage, while, in nature, the figure does not appear in such regular way, but always shows more or less modification. Not only so, but the considerable amounts of the nucleolar substance which thickly surround the chromatic figure tend to obscure the details of its arrangement. Fig. 13 is one of the best figures ever observed in the preparation in such a stage. In Fig. 14, the chromatic rods are not shown entirely but only a part. The rest of the structures of the cell-body remain in the same condition in which they were during the last stages of the prophase.

*C. Germinal Cells in the Anaphase.* The important changes in the chromatic figure in this phase are (1) the transverse splitting of the equatorial plate passing through the enlarged knobs which were primitively extremities of the dumb-bell; and (2) the pulling up of the chromatin from the equator toward each pole as a result of the contraction of the "Halb-spindelfasern." A very important, as well as interesting point, is the transverse splitting of the entire chromatic figure along the equator. Each of the portions resulting from this division forms a continuous spireme. Although the mitotic figures presented by the nerve cells show certain peculiarities in detail, still they agree exactly with the results obtained by previous investigators in that the chromosomes are divided into two exactly equal halves.

Fig. 16 is a first stage in this phase, and shows the first formation of the central spindle. The central spindle is evidently formed from two different substances. One of these is the linin, which intimately ensheaths the chromosome and the other is the nucleolar substance. The nucleolar substance does

not lose its peculiar staining character, showing always the same intensity of the color. By this character it can easily be distinguished from the other substance. The linin, on the other hand, stains very faintly, but slightly deeper than the cytoplasmic reticulum. According to LEVI, the nucleolar substance (acidophile part), forms only the "Halbspindelfasern," while the central spindle is formed by the linin alone. Our preparations however, show that the latter is not formed by the linin only, but also by the acidophile substance of the nucleolus. When two daughter chromosomes retreat toward opposite poles, then they are connected by delicate filaments composed of both linin and nucleolar substance. In most cases, the nucleolar substance can be detected very easily, since this substance clings to the linin filaments of the central spindles forming thick masses of irregular outline (Figs. 16 and 17). Another important and conspicuous change affects the cell-body which is transformed from the primitive spherical to the oval form.

Following the stage shown in Fig. 16, there is retraction of the two groups of daughter chromosomes toward their own poles (Fig. 18) until they reach two centers of the oval body (Fig. 18). Fig. 18 is a last stage in the anaphase, and presents the beginning of the division of the cell-body. The central spindle is still noticeable in this figure. From this stage on, the central spindle loses its affinity for the coloring reagents employed in this investigation, and at the same time loses the regular parallel arrangement of its filaments which re-form into the cytoreticulum.

*D. Germinal Cells in the Telophase.* Fig. 19 is one of the newly formed daughter cells, containing half of the chromosomes formed in the dividing cell. When the cell-body has been divided into two, then the regressive processes take place in each daughter chromosome, that is, the chromatic figure which presents an arrangement similar to that of the last stage of the anaphase (Fig. 18) is transformed gradually into that of the nucleus in the resting stage. Fig. 19 shows one of the daughter cells in the earliest stage of the telophase. The

chromatic figure is exactly similar in its principal characters to that of the preceding stage (Figs. 16, 17). In this stage, the nuclear membrane has not yet formed and the nucleolar substance surrounds the figure thickly in an irregular manner. In a far more advanced stage, however, the chromatic figure modifies itself in a remarkable manner, presenting a spiral arrangement along the periphery of the nuclear membrane (Fig. 20). The continuous chromosomes which present a spiral arrangement are constricted at intervals along their course, and divide the spiral line into numerous small segments. The linin could not be distinguished from the nucleolar substance. This stage is shown by Fig. 20. Following changes in the chromatic substance, the nuclear substance re-integrates and produces numerous acidophile granules (Fig. 21). In the next following stage the spiral arrangement of the filament ceases to be visible, but instead of that a reticular arrangement reappears in the nuclear area. The chromatic granules which were constricted from the continuous spiral line, diminish in size to a considerable degree and remain suspended in the reticulum (Figs. 21-23).

The filaments which form the reticulum just mentioned are not the same substance that forms spiral thread (Fig. 20); that is, the nucleolar substance which forms part of the sheath of the chromosome in the preceding stage—not shown in Fig. 20—forms scattered granules which, like the chromatic granules are suspended in the reticulum. The reticulum itself is composed entirely of linin substance. The scattered acidophile particles (nucleoli) are always larger than that of chromatic granules and further they stain a deep blue in the preparations made by HERMANN's method. This stage is shown in Fig. 21. Large spherical bodies are distinguishable here and there in the figure which represent the scattered acidophile particles of nucleolar substance. These scattered acidophile particles, however, sooner or later are collected (Fig. 22) at one point in the nucleus, generally at the center, although, in many cases, they remain in the scattered form, and do not centralize. Or, very frequently, some of these scattered acidophile particles centralize themselves while the rest of them remain in their original

places (Fig. 23). When the acidophile particles centralize themselves at one place, a circular space is produced. This space, however, appears to be filled by a fluid which also stains a red color after HERMANN'S method. In a further advanced stage, these groups of the acidophile particles, with enclosed liquid, are covered by another chemical substance which stains a blue color by HERMANN'S method. This latter substance seems to be derived from chromatic substance, because, in this stage, the latter material accumulates around the former. The present writer observed also, in most cases, extremely delicate filaments which directly arise from each acidophile particle and further, these filaments fuse together. The significance of these filaments just mentioned will be discussed later on.

#### IV. *Comparison with results of other investigators.*

From the preceding descriptions of the mitotic figures, it is clear that during the mitosis of the nerve cell the arrangement of the chromosomes as well as the behavior of the nucleolus is slightly different from that described in other kinds of cells by previous investigators.

FLEMMING<sup>1</sup> first described a peculiar modification of the mitotic figures which is clearly visible in the spermatocytes of the salamander. According to this author, the chromosomes in an early stage of the mitosis do not split entirely, but remain undivided at both ends, thus forming an oblong figure. Each oblong divides again transversely into equal parts and forms U-shaped chromosomes which lie in corresponding positions on each side of the equatorial plane. This U-shaped chromosome is not single, but is formed by two daughter chromosomes which are connected at their tips. To this kind of mitotic figure, FLEMMING has given the name "Heterotypical division or mitosis."

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<sup>1</sup> FLEMMING: Neue Beiträge zur Kenntniss der Zelle: *Arch. f. Mikroskop. Anatomie*, Vol. XXIX, 1887.

In most cases, the U-shaped chromosomes divide again lengthwise, and the four chromosomes of the same shape are produced from a single oblong. This phenomenon is known as "tetrad" formation of the chromosomes.

FLEMMING's observation was soon confirmed by many investigators and was also extended by HAECKEL on the germinal tract and urogenital cells of *Cyclops*; by VAN DER STRICHT on the *Thysanozoon* eggs; by v. KLINCKOWSTRÖM on the *Prostheceraeus* eggs, etc. In each case, the "tetrad" formation of the chromosome is somewhat similar in its principle to that of the salamander (FLEMMING), although there occur slight morphological differences.

The mitotic figure in the nerve cell may be regarded as one of the modifications of the heterotypical mitosis. A slight difference between the nerve cell and the case of the salamander is the following: The chromosomes in the nerve cell are always continuous throughout the entire course of division, while in the salamander the chromosomes divide into numerous segments which are separated from one another and perform the dividing processes independently. For this reason, the process of the mitosis is more difficult to follow in the nerve cells.

Although typically the chromosomes form a continuous thread, the present writer noticed occasionally somewhat V-shaped chromosomes which had been separated from the continuous group. The writer expects in the near future, to explain these peculiar cases.

#### *V. Morphology of the nucleolus.*

As has been already mentioned, the nucleolus of the nerve cell not only plays an important rôle in mitosis, but also presents a peculiar behavior when compared with that of other tissue as described by different authors. This peculiarity, however, depends on the special structure of the nucleolus in the nerve cell. At the later stage of the telophase, the nucleolar substance which intimately surrounds the chromosomes with a thick layer is dissolved and accumulated at certain places in the nucleus forming small spherical masses. These isolated masses in most cases aggregate themselves at the center of the nucleus and form a large group.

The nucleolar granules thus grouped give out one process from each pole. The processes fuse with one another, thus



forming a complete circle of the nucleolar substance (Fig. 22, 23). In the adult stage, more processes are produced. These in turn fuse until there is formed a very complicated network. This latter phase of the nucleolus can easily be seen in the nucleolus of the resting nucleus (Figs. 25, 26, 27).

Sooner or later, after the acidophile particles have been accumulated at one point within the nucleus, the basophile substance, as well as the linin surrounds the acidophile particles intimately. These three different substances, which are centralized in the nucleolus, can be beautifully demonstrated in the embryonic tissues which stain properly. This preparation shows us the acidophile substance staining red; the linin a faint red and the chromosomes a deep blue after HERMANN'S method. The nucleolus of the adult nucleus does not show these distinctions clearly, since the basophile substance accumulates about the periphery of the acidophile particles in great quantity and obscures them.

Fig. 25 is a nucleolus taken from a spinal ganglion cell of the gray rat. The material was preserved with the author's sublimate mixture,<sup>1</sup> followed by toluidin blue and erythrosin. In this case the chromatic granules, as well as nucleolus as a whole, stain bluish; while the acidophile particles stain deep blue. The number of the granules is variable even in the same kind of cells.

Fig. 26 is a nucleolus of the same animal preserved with CARNOY'S fluid followed by the same counter-stains. In this, the granules are much more numerous than the former. Fig. 27 is a nucleolus taken from the efferent neurone of *Torpedo occidentalis* which was preserved with 10% formalin stained with toluidin blue and erythrosin. In this case, we can see the similar granules in the nucleolus. VON LENHOSSÉK<sup>1</sup> distinguished a group of from three to five punctiform strongly

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<sup>1</sup> HATAI, S.: The Finer Structure of the Spinal Ganglion Cells in the White Rat. *Journ. Comp. Neurol.*, Vol. XI, No. 1, 1901.

<sup>1</sup> V. LENHOSSÉK: Die feinere Bau des Nervensystems im Lichte neuester Forschungen, *Berlin*, 1895.

stainable particles in the nucleolus which he termed "endonucleoli," but he makes no mention of their significance. Our figures of the internal structure of the nucleolus correspond exactly to that of VON LENHOSSÉK and therefore we identify the acidophile particles with the endonuclei of VON LENHOSSÉK.<sup>1</sup>

The following is a brief sketch of the investigations on the structure and staining reactions of the nucleolus.

FLEMMING<sup>2</sup> regards the nucleolus as composed mostly of the chromatic substance.

ROSIN,<sup>3</sup> who employed BIONDI's stain, maintained that the nucleus as well as nucleolus are neutrophile.

RAMÓN Y CAJAL<sup>4</sup> maintains that the nucleolus is composed entirely of nuclein which, however, was modified in the central portion by long mitotic repose. LEVI<sup>5</sup> has shown that the central part of the nucleolus stains with the acid color, while the periphery of the organ takes a basic color. From the above fact he concluded that the nucleolus of the nerve cells is composed of two entirely different substances; one of these is acidophile and the rest is basophile.

VAN GEHUCHTEN<sup>6</sup> holds the same view as CAJAL, maintaining that the nucleolus is composed entirely of chromatin. BÜHLER<sup>7</sup> described the nucleus of the spinal ganglion cells of

<sup>1</sup> LEVI was unable to see these granules, which were referred to by v. LENHOSSÉK, in his preparation (See Alcune particolarità di struttura del nucleo delle cellule nervose: *Rev. di. patol. nerv. e. ment.*, 1896, f. 4.)

<sup>2</sup> FLEMMING: Bau der Spinalganglienzellen. *Festgabe f. Henle, Bonn*, 1882.

<sup>3</sup> ROSIN: Ueber eine neue Färbungsmethode des gesamten Nervensystems nebst Bemerkungen über Ganglienzellen und Gliazellen. *Neurol. Centralbl. Leipzig*, Bd. xii, 1893.

<sup>4</sup> RAMÓN Y CAJAL: Estructura del protoplasma nervioso. *Rev. trimest. Microg., Madrid*, Vol. I, 1896.

<sup>5</sup> LEVI, G.: Considerazioni sulla struttura delle nucleo delle cellule nervose. *Rev. pat. nerv. e ment.*, III. 289-296, 1897.

<sup>6</sup> VAN GEHUCHTEN: L'anatomie fine de la cellule nerveuse, *Neurolog. Centralbl.*, 1897, p. 905, and *Revue Neurologique*, 1897, p. 494.

<sup>7</sup> BÜHLER: Untersuchungen über den Bau der Nervenzellen. *Verh. der Physik. med. Gesselsch. zu Würzburg*. Bd. XXXI, Nr. 8, '98.

the frog as composed of oxychromatin in very abundant quantity and small amount of basichromatin. He also said that the nucleolus is composed of a substance very similar to the basophile substance of the nucleus, but not identical with it.

TIMOFEEV<sup>1</sup> observed two kinds of nucleoli in the nucleus of the nerve cells of birds, one of which exactly corresponds in its structure to that described by LEVI; while the other is entirely acidophile.

*VI. Critique of the observations of previous authors on the nucleolus.*

From the above descriptions, we can distinguish two entirely different views concerning the structure and staining reactions of the nucleolus. One of these is represented by LEVI, who regards the nucleolus as composed of two substances, basophile and acidophile. The other is represented by CAJAL and VAN GEHUCHTEN, who believe the nucleolus to be merely a modification of the basophile substance, which has resulted from long mitotic repose.

In the analysis of the cells by histological methods, it is evident that these methods which give the highest degree of differentiation are the ones which should be made the basis of our description. Hence we are justified in following the descriptions of those authors who have been able to obtain the highest degree of differentiation in the cells which they studied and in disregarding the views which have been developed on the basis of negative results.

The results obtained by ROSIN, who states that the nucleolus and nucleus are neutrophile are, no doubt, due to the less differentiation of the stains which were employed by him.

The present writer also questions the conclusions drawn by CAJAL and VAN GEHUCHTEN, because these investigators used only methylen-blue after NISSL. By this method it is absolutely impossible to distinguish the different substances in the

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<sup>1</sup> TIMOFEEV: Beobachtungen über d. Bau der Nervenzellen d. Spinalganglien u. d. Sympathicus beim Vogel. *Internat. Monatschr. f. Anat. u. Physiol.*, 1898, H. 9.

nucleus as well as the nucleolus, since methylen-blue, especially after NISSL's technique, colors all the structures a deep blue.

Not only the technique employed, but the age of the animal modifies these staining reactions. The present writer obtained the following results from the resting nucleus of the nerve cells of the adult white rat which had been preserved with CARNOY'S fluid followed by toluidin blue and erythrosin: namely, the chromatic granules, as well as nucleolus, were stained bluish-color of equal intensity. Using the germinal cells of the white rat in an embryonic stage, the tissue having been preserved and stained in the same manner as that of the adult animal, it was found that the chromosomes only stain a deep blue, while the nucleolus appeared a deep red.

The present writer agrees with the view of LEVI in so far as he describes the nucleolus as a group of the acidophile particles which are surrounded by the linin. But in addition to the linin, LEVI considers that the basophile substance also surrounds the acidophile particles. To the last statements the present writer cannot agree, because in this case the basophile substance is merely an accumulation, surrounding the nucleolus, and further this hollow sphere formed by the basophile substance is clearly separated from the linin which directly surrounds the acidophile particles. From this, we cannot regard the basophile substance as one of the structural parts of the nucleolus, but simply as lying outside of it.

TOUCHE and DIDE<sup>1</sup> obtained a result similar to that of LEVI, stating that the nucleolus is composed of basophile and acidophile particles. The present writer, however, concludes from their figures that the nucleolus can hardly be regarded as composed of the two substances just mentioned, because, as their figures show, the basophile particles are separate from the acidophile substance. Figs. 1 and 3 of the same paper show separation of the basophile particles from that of the acidophile. The rest of the drawings also show evidently a simple attachment of the basophile particles to the acidophile.

<sup>1</sup> TOUCHE et DIDE: Note sur la structure du noyau et de division amitotique des cellules nerveuse du Cobaye adulte. *Rev. Neurol.*, N. 2, 1901.

CAJAL<sup>1</sup> classified the nucleus of the nerve cells in three large groups. The third type of the nucleus, according to him, is noticeable among the large nerve cells; motor neurones, spinal ganglion cells, cells of PURKINJE, giant pyramidal cells, etc. In these classes of cells, the nucleus is pale, containing the nuclear sap and traversed by a network in which the knobs never carry the chromatic granules. The chromatic granules concentrate themselves surrounding the single voluminous nucleolus and form a perfect spherule. Although his description is not universally applicable, the present writer has observed very often such nuclei as those described by CAJAL in the large somatochrome cells. In these nuclei the basophile granules centralize themselves, surrounding the nucleolus, thus forming compact spherical masses composed of acidophile and basophile substances. This fact offers a very favorable opportunity to determine whether the basophile granules which surround the acidophile substance of the nucleolus can be regarded as one of the structural parts of the latter organ, because in such cases, if LEVI's statement is right, how can we distinguish the basophile particles which were regarded by him as one of the structural parts of the nucleoli from the other part of the basophile? It is impossible to distinguish these, since they are nothing more than degrees of centralization of chromatic granules. The present writer therefore concludes that the nucleolus is a group of the acidophile particles which is surrounded by the linin.

### VII. *Summary.*

In the cerebellar cortex of the foetal cat, a study of the largest germinal cells shows:

1. The germinal cells of the nervous system of the foetal cat present a modified form of the heterotypical mitosis of FLEMMING.
2. The number of the chromosomes represented by inter-nodes of segmented filaments is 16.

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<sup>1</sup> RAMÓN Y CAJAL: Loc. cit.

3. All of the "Halbspindel," as well as a part of central spindle, are derived from the nucleolar substance, the central spindle containing the linin in great abundance.

4. The nucleolus is composed of acidophile particles surrounded by the linin, as brought out by HERMANN'S method.

### VIII. Illustrations.

The following are freehand drawings, using oil immersion lens (Obj. L. 16  $\times$  Ocular, B & L. 1). The sizes of the cell-bodies as well as those of the nuclei were given in the text.

#### PLATE XVIII.

*Figs. 1-10.* Germinal cells in the prophase. Cerebellar cortex of foetal cats; RIPART et PETIT; HERMANN'S, Figs. 3 and 9; GILSON'S fluid; HERMANN'S.

*Figs. 11-15.* Germinal cells in the metaphase. Cerebellar cortex of foetal cats; RIPART et PETIT; HERMANN'S Fig. 14; GILSON'S fluid; HERMANN'S.

*Figs. 16-18.* Germinal cells in the anaphase. Cerebellar cortex of foetal cat; GILSON'S fluid, HERMANN'S.

*Figs. 19-24.* Germinal cells in the telophase. Cerebellar cortex of foetal cats. GILSON'S fluid; HERMANN'S.

*Fig. 25.* Nucleolus of the spinal ganglion-cells of gray rat. The author's sublimate mixture, toluidin blue and erythrosin. 3.2 micra  $\times$  3.2 micra.

*Fig. 26.* Nucleolus of the spinal ganglion cell of the adult white rat. CARNOY'S fluid; toluidin blue and erythrosin. 3.2 micra  $\times$  3.2 micra.

*Fig. 29.* Nucleolus of the efferent neurone of the electric organ of *Torpedo occidentalis*. 10% formalin; toluidin blue and erythrosin. 5.7 micra  $\times$  5.7 micra.

# THE DIVISION OF DIFFERENTIATED CELLS IN THE CENTRAL NERVOUS SYSTEM OF THE WHITE RAT.

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With Plates XIX, XX.

## PART I. NUMBER AND POSITION OF THE DIVIDING CELLS.

The investigations which form the subject matter of this paper were undertaken in connection with a series of studies on the development of the central nervous system of the white rat, now being carried on in this laboratory.

At the outstart the question to be solved related only to the number and distribution of the dividing cells in the central nervous system of the new born white rat, but in the course of the investigation other problems suggested themselves and led to a study of the character of the dividing cells as well.

The white rat was chosen as material because of the abundant data relative to its development, which were already available in the laboratory, and also because of the immature condition of the nervous system at birth. The study was not, however, confined to the new born rat, although the investigations upon the animal at this stage were more extensive than those made upon earlier and later stages. Foetuses of about 17 mm. in length<sup>1</sup> were examined, and also rats 1, 2, 3, and 4 days old.

The material was hardened in GRAF'S fluid,<sup>2</sup> and in FLEM-

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<sup>1</sup> The aggregate weight of the 4 foetuses examined, was 3.09 g., each foetus being about 17 mm. in length.

Oxalic acid 8%, 4 vols.  
Alc. 95%, 3 vols.  
Chromic acid,  $\frac{1}{2}\%$  3 vols.

MING's solution, the former giving the best results. It was imbedded in paraffin, and stained with iron-lack-haematoxylin, either alone or with erythrosin as a counter-stain, with saffranin and with toluidin blue and erythrosin. One series from the new-born rat was carried through by VIGNAL's method; i. e. alcohol-osmic acid hardening, picrocarminate of ammonia stain, —this method being said by VIGNAL to demonstrate the character of the cytoplasm and processes unusually well. Unfortunately it does not stain the mitotic figures, so that it was not of much value for this study, except that it showed with great clearness the different forms of glia cells. GRAF's fluid and iron-lack-haematoxylin gave the most satisfactory results.

The cord and cerebral hemispheres of the new-born rat were first studied, and therefore the results obtained from them will be given first.

The cord of the new-born rat contained a large number of mitoses, which were found chiefly in the outer layers; the number on the ventricular surfaces was suprisingly small. In the brain the ventricular mitoses were more numerous than in the cord, but here also the extra-ventricular predominated. The brain and cord of the 24-hour rat contained fewer mitoses than the new-born rat, while in the three days and four days old specimens the number seemed equal to that of the new-born. Comparing the foetus with these older specimens, a striking difference was seen, for here the mitoses seemed to be predominantly on the ventricular surfaces. Figs. 1, 2, 3, 4.

In order to decide the question beyond doubt the mitotic figures were counted in 15 sections,  $6\frac{3}{4}\mu$  in thickness, taken from the cerebral hemispheres and from the cervical, thoracic and lumbar regions of the cord of the new-born rat. Also from the cerebral hemispheres and lumbar cords of the foetus and of the 24-hours and four day specimens. The sections of the hemispheres were coronal and taken at the level of the chiasma. The following tables give the results of these counts.



TABLE I.

The Number of Mitoses in 15 consecutive Sections, each Section  $6.75\ \mu$  in thickness, from the Brain and Spinal Cord of Rats at Different Stages of Development.

Stage of Development.	Brain.	
	Ventricular Mitoses.	Extra-Ventricular Mitoses.
Foetus	2196	966
Birth	390	595
24 hours	24	386
4 days	115	443

	Lumbar Cord.	
	Ventricular Mitoses.	Extra-Ventricular Mitoses.
Foetus	28	18
Birth	8	45
24 hours	1	13
4 days	8	64

Cell division seems to reach its lowest ebb at the end of the first day. After this it slowly rises, until by the end of the fourth day, when the number of mitoses is not much behind that found at birth.

These tables show clearly the actual diminution in the mitoses as development proceeds, and the relative increase of the extra-ventricular mitoses over the ventricular. This relative increase reaches its height at the end of the first twenty-four hours, when the ventricular dividing cells are very few. After that there is an increase in mitoses in both regions, but slightly greater on the ventricular surfaces than in the outer layers. This relation of the numbers in the two regions may be seen in the following table :

TABLE II.

The Relative Number of Extra-Ventricular Mitoses Expressed as a Ratio. Based on the Observations on the Lumbar Cord given in Table I.

		Lumbar Cord.	
		Ventricular.	Extra-Ventricular.
Foetus	1	to	0.6
Birth	1	to	5.4
24 hours	1	to	13.
4 days	1	to	8.

Although the actual number of mitotic figures varies appreciably in different animals from the same litter, which apparently are at constant stage of development, yet the proportion

between the ventricular and the extra-ventricular mitoses remains practically constant for the same stages of growth.

A comparison between the different levels of the cord was made only in the case of the new-born rat.

TABLE III.

Observations Based on 15 Consecutive Sections, Each Section  $6\frac{3}{4}\mu$  thick, from the Cervical, Thoracic and Lumbar Portions of the Cord of the New-Born Rat.

	Cord of New-Born Rat.	
	Ventricular.	Extra-Ventricular.
Cervical	1	26
Thoracic	3	20
Lumbar	8	45

The lumbar cord resembles the cord of the foetus in the large number of mitoses, and in the relatively large number on the ventricular surfaces, while the thoracic cord shows a relative increase of extra-ventricular dividing cells, which is still more marked in the cervical cord.

From the lumbar cord in the same series, 25 sections were examined, in order to determine the exact distribution of the mitotic figures.

TABLE IV.

Showing the Distribution of Mitoses in the Lumbar Cord of the New-Born Rat, from Observations on 25 Consecutive Sections, each  $6\frac{1}{4}\mu$  in Thickness.

Lumbar Cord of New-Born Rat.	
Anterior gray column	61
Posterior gray column	25
Fiber tracts	8
Ependyma	10 <sup>1</sup>

In the distribution of the mitoses throughout the cord, the anterior horns of the gray matter seem to be the "seat of predilection" in the new-born rat, the posterior horns following far behind. No counts were made in the older specimens to determine the exact distribution, but judging from a careful examination, it is the anterior horns here also in which the greater number of mitoses are found.

<sup>1</sup> This number is slightly smaller than would be expected from the examination of the 15 sections of the lumbar cord given above.

This question as to the situation of the dividing cells and incidentally, the period up to which they persist in the central nervous system has been dealt with by ALTMANN (1881), RAUBER (1881-82-86), MERK (1886), HIS (1886), VIGNAL (1889), SCHAPER (1897) and by PATON (1900).

ALTMANN (1) was the first to point out the ventricular situation of the dividing cells and laid down the rule that in all organs of epithelial origin, cell division takes place on one surface only, that farthest removed from the mesoderm. HIS (2) confirmed this statement in his study of the human embryo of one month. RAUBER (3), on the contrary, denied any "seat of predilection" for the dividing cells. In his earlier publications he takes a more decided stand than in his later, but in all he insists that no layer of cells is exclusively the seat of cell division, and that the distribution of mitotic figures varies greatly, predominating now in the innermost layer, now in the outer layers. At one stage, for instance, in the spinal cord, the largest number is found in the anterior horns of the gray matter. His researches on frog embryos of 4.6 mm. and of 15 mm. show that at both these stages the ventricular mitoses predominate, but extra-ventricular ones always are present. He explains the apparently contradictory views held by different observers on the ground that the material used represented very different stages of development.

MERK (4) worked on embryos of fish, amphibia, birds and mammals, including rats. He upholds ALTMANN'S view very strongly, and although he admits that scattered mitotic figures are in some instances found, yet those situated on the ventricular surfaces are always—in the cord and cerebral hemispheres—very much in the majority. An exception is found in the early stages of development in fish and amphibia, where for a short time, cell division is equally distributed in all layers.<sup>1</sup> But in the higher vertebrates from the time of the closure of the

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<sup>1</sup> It is remarkable that MERK found the diffuse arrangement of the mitoses in the early stages, while most observers, as will be seen, find this, if at all, in the later stages.

medullary tube, up to the period represented by the 9 day chick, all mitotic figures in the cord are around the canal; all, with a very few exceptions, in the brain are around the ventricle. He counted the mitoses in 25 sections of both cerebral hemispheres of a mouse embryo, 2-3 mm. in length and found 50 ventricular mitoses to 1 extra-ventricular. In the cerebellum and basal ganglia, however, he finds the mitoses always scattered and he considers that this fact is connected with the rapid growth of these parts of the central nervous system. Wherever growth is slow, as in the cord and hemispheres, cell division takes place around the ventricle,—wherever it is rapid, as in the cerebellum, thalamus and corpus striatum, cell division occurs in all layers of cells. This division of cells, he finds, ceases in birds and mammals at about the time when a posterior median fissure is clearly to be seen, or when the canal has become circular and the ependymal cells are provided with cilia.

VIGNAL (5) takes a stand different from either of the above. He finds that in embryos of chicks, rabbits and sheep, the mitotic figures are only in the ependymal layer nearest the ventricle, but does not therefore conclude that cell division is confined to this region. On the contrary, he considers that the greater part of it takes place in the gray matter. He explains this apparent contradiction by assuming that these cells divide, not by mitoses, but by the formation of "achromatic figures." Naturally a description of such figures cannot be given, but as the nucleus, when dividing enlarges and loses some of its chromatin, the author considers that it is possible to distinguish the dividing cells from the resting ones. He is led to this belief by his failure to find mitotic figures in the developing cord anywhere except directly around the canal (although he treated his material by FLEMMING's method), and as there is every evidence of a more rapid increase in the number of cells than can be accounted for by the few ventricular mitoses, it follows that the cells must divide in some other way than that usually described.

SCHAPER (6) confirms ALTMANN's dictum as to the ventricular predilection of mitoses, but only for the earlier stages of

development, before the blood vessels have formed. He believes this to be true of all hollow organs lined with epithelium; cell division is at first most active on the surface lining the cavity, both because here the resistance is lessened and because, in all probability, the fluid in the cavity serves as nutrition for the new cells. Later on, however, when the development of the blood vessels has taken place and the nutrition is equalized, the extra-ventricular mitoses appear.

PATON (7), working on the brain of pig embryos, finds very few extra-ventricular mitoses and considers their occasional appearance a phenomenon of little importance.

The contradictory results obtained by these different authors may perhaps best be explained as RAUBER explained them, by the fact that they were obtained from embryos representing widely different stages of development. It may be that those who found cell division confined to the ventricular surfaces were studying much younger than those who found mitoses scattered through the gray and white matter. It is difficult to determine corresponding stages of development in different animals when only measurements are given, especially as in some instances the fresh, in others the hardened embryo is measured, but drawings of the cross sections of brain and cord make it possible to compare the stages with some degree of accuracy. MERK's drawings for instance, are most of them from quite early embryos, the germinating layer is very wide, the nerve cells immature, and therefore it is not remarkable that extra-ventricular mitoses were very few. One drawing of the cord, however (Fig. 5) and one of the brain (Fig. 2) shows a stage of development which is represented by the foetal rat in my series. In MERK's drawings the mitoses are seen to be confined to the ventricular surfaces—in the embryo rat in my series the ventricular mitoses predominate, but each section contains two or three dividing cells in the outer layers. Another drawing in MERK's article is from the cord of a  $7\frac{1}{2}$  day chick (Fig. 10) when the stage of development is about midway between the foetal and new-born rat in my series. Even here no extra-ventricular mitoses are shown.

VIGNAL's results are still harder to bring into harmony with mine, for his illustrations show all periods of development from the long narrow tube with only the germinating layer of cells, to the fully formed cord with definite groups of multipolar cells, but throughout the series he finds not one extra-ventricular mitosis.

Although RAUBER himself suggests that the variation in number and position of the dividing cells is due to the period of development of the embryo in question, yet apparently he finds no difference between his frog embryo of 4 mm. and the one of 15 mm.

PATON gives drawings (see his Figs. 4 and 6) from pig embryos which correspond to the brain of the foetus and of the new-born in my series, but he finds very few extra-ventricular mitoses in either; only one is represented in his drawings. Even SCHAPER, although he mentions the appearance of these extra-ventricular dividing cells as coincident with the development of the blood-vessels, apparently does not attach much importance to them, as he gives no description of their number, nor of the exact areas in which they are found. There is no mention anywhere in the literature of dividing cells being found in the nerve fiber tracts.

It might be suggested that the grade of the animal in the zoological series is an important factor, that in the lower vertebrates the course of development is different from that in the higher, and this may be true, but so far there is not much in the literature to confirm it. HIS, working on early human embryos, arrives at the same conclusions as MERK, who uses embryos of fish, amphibia, birds and mammals.

MERK alone makes an absolutely definite statement as to the period at which cells cease to divide. According to him, the dividing cells gradually diminish in number and disappear by the time the central canal has become circular, the ependymal cells ciliated, and the posterior median fissure formed. This represents a stage which the cord of the white rat has attained at birth.

To recapitulate the points in which the results of this study

of the central nervous system of the white rat differ from those arrived at by the observers quoted above :

1st. The ventricular mitoses predominate only in the earlier stages of development, while the nerve fiber tracts are still very narrow, the layer of germinating cells wide and the nerve cells immature. Even at this stage, numerous extra-ventricular mitoses are found.

2nd. As development proceeds, there is a relative increase of extra-ventricular mitoses, so that by the end of the first day after birth, they are greatly in the majority. After this and up to the end of the 4th day, there is a slight proportional increase of the ventricular mitoses again.

3rd. Cell division does not diminish steadily, but reaches a low point at the end of the 1st day and then rises again. This corresponds to the general suspension of growth in the whole animal just after birth and the gradual increase after that. The cells continue to multiply for at least four days after the stage described by MERK, and at the end of the fourth day the mitoses are more numerous than at the end of the first.

4th. The extra-ventricular mitoses are found chiefly in the gray matter, especially in the anterior horns, though a few are in the fiber tracts.

## PART II. NATURE OF THE DIVIDING CELLS.

In the course of the determination of the number and persistence of mitoses in the central nervous system of the white rat, certain peculiarities in these dividing cells were noticed which led to a closer study of the nature of these cells found in the different localities. A brief examination of the cord at birth and for four days after birth is enough to convince one that the dividing cells are not all alike, that on the contrary, they differ in size and shape, in the character of the cytoplasm and in the thickness of the chromosomes. The variations in size are not so marked in the dividing cells of the brain as in the cord, but they are appreciable, and the other differences are as clearly marked as in the cord. In the brain and cord of the foetus the majority of the dividing cells are of one kind

only, and at first sight one does not notice any striking difference, but a more careful study reveals almost as many types of dividing cells here as in the later specimens. It will be more convenient to describe these cells as they are found in the different cell layers, rather than at the different stages of development, for the character of the dividing cells is very much the same in the corresponding localities in both early and late specimens.

Taking first the ependyma of the cord, we find that the great majority of the dividing cells are of the kind described by His as germinal cells,—round or oval cells, measuring, in the white rat, from  $7.5 \times 6 \mu$  to  $12 \times 10.5 \mu$  (Fig. 5). These cells usually lie directly bordering on the canal, but in the cord of the foetus they may be the distance of one or two cell layers from the edge. In the cord after birth the germinal cells are usually smaller than in the foetus. These germinal cells form the majority of all dividing cells in the foetus and are found in appreciable numbers around the ventricles in the later specimens. They are found in all the stages of mitosis, but, except for the different arrangement of the chromosomes, they show no great variations. There are, however, occasionally dividing cells in the ependyma of the cord which cannot be classed with these typical germinal cells, but which differ greatly from them. These are long cells, much larger than the typical germinal cells of His, pointed at one or at both ends and in several instances sending a process to the internal limiting membrane of the canal (Figs. 6, 7), the cell shown in Fig. 6 measuring  $24 \times 7.5 \mu$ . These long pointed cells are situated always at the ventral and dorsal extremities of the canal, in the region of the ventral and dorsal plates of His, where, according to His, no neuroblasts are formed, the ventral plates becoming converted into neuroglia, the dorsal filled with spongioblasts. Certainly these cells are not the germinal cells of His, but resemble in every way, except their great size, the spongioblasts which are so abundant in these regions. It is interesting to note in this connection that, as the development of the cord proceeds, the dividing cells around the canal tend



more and more to lie at the dorsal and ventral ends of the canal, at the points, in other words, where the spongioblasts persist after they have disappeared from the remainder of the ependyma. No such long pointed dividing cells are found in the ependyma of the brain, the mitoses here are all found in round or oval cells, and lie usually in the layer directly bordering on the ventricle. In the brain of the foetus the ependyma consists of many layers of cells, and it is not uncommon to find germinal cells at quite a distance from the ventricle, but in the brain of the new-born rat the ependyma is reduced to two layers, and the typical germinal cells, now much diminished in number, are found only in these two layers.

The dividing cells in the gray matter of both cord and brain are more numerous in the later specimens, but the same types are found in all. It is here in the gray matter that the greatest variations are found; variations in the size of the nucleus and the character of the chromosomes, in the amount of cytoplasm and the shape of the cell-body. These cells may be roughly divided into two groups, those with no visible cell body, and those with a well developed cell body.

The cells of the first class are very numerous in the later specimens, more so than in the foetus. They are comparatively small, measuring about  $6 \times 3 \mu$  (Fig. 8b), but even in the largest there is no visible cell-body, and the chromosomes are comparatively delicate (Figs. 8, 9, 10).

A much greater variety of cells belong the second class, the cells with a well developed cytoplasmic body. These are numerous in the gray matter of both cord and brain at birth and after, but less abundant in the foetal brain and cord. They therefore increase in number as the development of the gray matter proceeds. Their size varies from  $10 \times 7 \mu$  (Fig. 11, A) to  $18 \times 12 \mu$  (Fig. 12, A). They are round or oval usually but may be pear shaped (Fig. 12) or spindle shaped (Fig. 13). The chromosomes are thick and heavy, the cytoplasm is granular, staining deeply with saffranin or erythrosin, but often showing a clear zone around the nucleus. They lie among the neuroblasts in the foetal cord and brain and among the multi-

polar and pyramidal cells in the later specimens, and may be found anywhere in the gray matter from the outer edge of the ependyma to the outer edge in the gray matter. A comparison of the size of these dividing cells with the large nerve cells in their immediate neighborhood gives the following results:

Dividing cell in the anterior horn of the spinal cord at birth (shown in Fig. 12)  $18 \times 12 \mu$ .

Multipolar cell (Fig. 12, B)  $19 \times 11 \mu$ .

Dividing cell in cortex of brain at birth (Fig. 16, A)  $11 \times 8 \mu$ .

Nerve cell (Fig. 16, B)  $12 \times 7 \mu$ .

The size of these large dividing cells, therefore, corresponds very closely to that of the nerve cells in their neighborhood, while no other cell in the gray matter approaches them in size. The thin granular protoplasm staining deeply with erythrosin increases the resemblance to nerve cells.

In rare instances mitotic figures are found in cells which resemble in every way multipolar ganglion cells and which lie in the anterior horns of the gray matter in close proximity to the ganglion cells. Three such cells, from the three levels of the cord are shown in Figs. 18, 19 and 20. In Fig. 20 the chromosomes are not typical and the possibility of some degenerative change must be admitted, but the same cannot be said of those shown in Figs. 18 and 19. Here the arrangement of the chromosomes is perfectly normal. In size, shape, processes and cytoplasm, these dividing cells resemble the multipolar cells in these regions. It is only in the cord that these dividing cells with processes are seen. The mitoses in the cortex of the brain are found in cells which are not as large as the largest dividing cells of the cord (Figs. 15, 16, 17), are usually round or oval and in no instance in this region was a cell with processes found undergoing division.

The nerve fiber tracts are narrow in the cord of the foetus and in the hemispheres where they form a very narrow layer between the wide ependyma and slightly narrower cortex (Figs. 1 and 3). At birth the tracts in the cord have increased appreciably both anteriorly and laterally while in the brain they

form fully half the width of the section, the ependyma being reduced to a thin double layer. Within these tracts are found in the cord neuroglia cells of different sizes and, in the lateral tracts especially, scattered neuroblasts and multipolar cells. In the fiber tracts of the foetal brain there are, besides the neuroglia cells, many neuroblasts which are found lying diagonally and horizontally and vertically. Evidently the neuroblasts which are formed in the ependyma make a half revolution in this layer on their way to the cortical layer. Later stages show fewer neuroblasts, in the fiber tracts and finally—in the 4 days specimen—only neuroglia cells. The dividing cells in the white tracts are not very numerous at any stage of development, and when present they are usually of the same variety, without cytoplasm. Large ones are sometimes found in the anterior and lateral tracts of the cord, near the gray matter, but usually the mitotic figures are small and delicate.

It is evident that in the later stages of development the increase of cells in the central nervous system of the white rat does not take place through the division of one kind of cell only, that there is not an indifferent dividing cell, but several varieties of cells which may undergo division.

Referring to the literature on this subject one naturally begins with the classical work of HIS (2) on the central nervous system of the human embryo of one month.

According to HIS the original epithelial elements which line the neural tube become differentiated into two kinds of cells, only one of which is capable of multiplication. These are the germinal cells which appear among the epithelial as round or oval bodies measuring in man  $10 \times 14 \mu$ . The nucleus is usually in one of the stages of mitosis, but when resting has a thick nuclear membrane and scattered chromatin masses. These germinal cells divide in the layers of ependyma nearest the ventricle, and their offspring migrate from this region out toward the periphery, grouping themselves together to form the layer of cells which HIS called the mantle layer. During their passage, or after completing it, they undergo changes which result in the formation of neuroblasts, that is, the oval cell be-

comes pointed, the cytoplasm around the nucleus forms a long process at the extremity of the cell which is turned toward the periphery. The nucleus also changes, the nuclear membrane becomes less thick, the chromatin masses more delicate and a nucleolus appears. These neuroblasts never divide, neither do the supporting cells which constitute the second variety of cells found in the neural tube. They are long, narrow cells derived from the epithelium of the ependyma, which elongate and send out a process to the inner limiting membrane and another long branching process to the outer limiting membrane. These branching and anastomosing processes form the frame-work for the neuroblasts in the earlier stages, later on mesoblastic elements wander in and help to form the neuroglia.<sup>1</sup> The original supporting cells, which HIS called spongioblasts are in his opinion, incapable of division, and the increase in their number is not clearly explained inasmuch as he has never seen epithelial cells dividing to form new spongioblasts, and thinks it doubtful whether any of the offspring of the germinal cells become spongioblasts. He observed what seemed to be mitoses in some spongioblasts but thought such appearances should be looked upon with great suspicion.

This description of the germinal cell and of the formation of neuroblasts is accepted by the majority of histologists, by VON KÖLLIKER (8), by RAMÓN Y CAJAL (9), VON LENHOSSÉK (10), RETZIUS (15), KOLLMAN (11). The direct transformation of the epithelial cells of the surface of the body into germinal cells and of their offspring into neuroblasts, was observed by FLEXNER (12) in *Planaris torna*. After removal of the head including the head ganglia the epithelial cells underwent mitotic division and the new cells wandered into the deeper tissues and passed through the stages described by HIS, resulting in the formation of neuroblasts with axones.

On the question of the formation of the neuroglia, however, the original theory of HIS has received little support and

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<sup>1</sup> This explanation of the mesoblastic origin of some of the neuroglia has been withdrawn by HIS in his later papers.

he himself has abandoned it. The mesoblastic origin of the neuroglia cells is rejected by almost all histologists, and as the number of ependymal cells is not nearly large enough to account for all these cells, it is usually assumed that they must increase by cell division. The germinal cell of HIS, then, is considered by the authors mentioned above as a simple epithelial cell in process of division. It is not in any sense a specialized cell and gives rise not only to nerve cells, but also to the cells of the neuroglia. On the question of the exact mode of formation of the supporting cells, there is a difference of opinion. WEIGERT (13) and SALA Y PONS (14) both describe the gradual transformation of ependymal cells into glia cells as follows: The ependymal cell elongates and sends out two processes to end at the ventricle and at the periphery. Then by a gradual shortening of the peripheral process the cell is drawn out, away from the ventricle, it loses its connection first with the ventricle, then with the periphery, develops side processes and is converted into a spider cell. VON LENHOSSÉK (10) accepts this description of the formation of glia cells for some of the cells, but only for a few, as the number of ependymal cells is too small to account for all the spider cells found in the adult cord. Some undoubtedly are formed in this way, but the larger number must arise by division of the cells of the neuroglia. VON KÖLLIKER (8) also thinks it probable that glia cells divide.

The explanation of VIGNAL (5) differs from that of any other writer, not only by assuming a process of cell division which does not correspond with mitosis, nor amitosis as usually described, but also by denying any differentiation of cells in the central nervous system during the earlier stages of development. Thus, he considers not only the germinal cells indifferent, but all of the cells of the neural tube up to the time when a distinct grouping of the multipolar cells of the anterior horns can be seen. Until this time—a point represented by three and a half months in the human embryo—the cells have all been alike in spite of apparent differences in size, shape and staining reactions. Nerve cells, he maintains, cannot be distinguished from supporting cells until the dendrites are formed.

SCHAPER (6) has gone very exhaustively into this subject, and takes a stand midway between VIGNAL and the majority of observers. The original epithelial elements, according to SCHAPER, undergo one of two changes, either they are transformed to ependymal cells, which in higher vertebrates persist only around the ventricles, or they change to "indifferent" cells. As the ependymal cells are incapable of further multiplication, all increase in supporting cells and nerve cells must be through the division of these indifferent cells. At first these cells divide actively around the ventricles and the new cells wander out into the mantle layer. They are now the cells which by HIS were called neuroblasts, but SCHAPER considers them transition forms, not yet differentiated, capable of developing immediately into either supporting cells or nerve cells, or of dividing again and again without losing their indifferent character. Later on the formation and division of germinal cells around the ventricle gradually lessens and these indifferent cells in the mantle layer begin to divide. We have now in the mantle layer three kinds of cells: first the true neuroblast, with a large clear nucleus, darker nucleolus and axone; second the glia cells, small with no visible cytoplasm, darker nucleus with thick chromatin granules; third, larger cells with bubble-like nucleus, finely granular chromatin, no nucleolus and no visible cytoplasm. These last are the indifferent cells and are the only ones capable of multiplication. They persist up to a late period perhaps even into adult life, and it is by the division of these cells alone that nerve cells and also neuroglia cells are formed. In his description of the process of formation of the neuroblasts, SCHAPER follows HIS, but on the question of the development of the neuroglia he is not quite so clear. Some of the cells are accounted for in the way given by WEIGERT and SALA Y PONS, the migration and transformation of ependymal cells—others are formed by the division of the indifferent cells. But SCHAPER says that it is hard to account for the enormous number found in the adult, as the fully formed neuroglia cells are incapable of dividing.

In a recent article PATON (7) elaborates this theory of

SCHAPER. He too considers that the offspring of the germinal cells are indifferent, and may either develop into nerve cells or supporting cells or remain indifferent. PATON's work was on the brain of pig embryos. His description of the indifferent cells agrees with that of SCHAPER, but he finds them undergoing division almost invariably in the ependyma, not in the mantle layer. In all stages of development except the very early, PATON finds two kinds of germinal cells, one large with a well developed cell body, and one small with almost no cell body, but he thinks this difference is unimportant as both alike produce indifferent cells. Development proceeds first in the ependyma which grows rapidly and is filled with germinal cells, indifferent cells and the spongioblasts of HIS. The indifferent cells which are to become neuroblasts pass to the outer layer of the ependyma, and here or in the nerve fiber layer are transformed into neuroblasts and pass out to form the cortical cell layer. As for the supporting cells, they are at first represented by the spongioblasts of HIS—transformed ependymal cells which diminish in size and number as they wander away from the ventricle, persisting in higher vertebrates around the ventricle only. As they disappear, the glia cells appear, being the result of division of the indifferent cells.

It is evident that there is nothing in the literature on the development of the central nervous system which points to the occurrence of large extra-ventricular dividing cells such as are found in the brain and cord of the white rat, nor does any theory of the process of cell formation allow for the presence of such cells.

The germinal cells of HIS are described as always situated on the ventricular surface or separated from it by one layer of cells only. They have no large granular cytoplasmic body, and never have processes. SCHAPER has been already quoted as mentioning dividing cells in the gray matter, but these cells are, according to his description, invariably devoid of cytoplasm. Moreover, according to SCHAPER and to PATON, all of the new cells formed during the growth of the cord and brain are derived from the division of indifferent cells, which are of one

type only, and it is impossible to tell whether nerve elements or supporting cells will result from the division of any cell. Fully formed neuroglia cells, spongioblasts, neuroblasts and nerve cells are all, according to these two authors, incapable of multiplication. There is indeed practically unanimous agreement among histologists as to the impossibility of the fully formed nerve cells or supporting cells dividing, under normal conditions, whatever may be true of pathological conditions. SCHAPER expresses the general view when he says: "A new formation of nerve cells in the fully developed nervous system is impossible for the division and increase of such highly differentiated ganglion cells as exist in vertebrates at least, must be rejected. Not only is a cell which is morphologically so highly differentiated incapable of dividing by karyokinesis, but it is impossible that a nerve cell should suspend its physiological activity and with it that of a whole chain of neurones, during a period when the nuclear substance must be entirely devoted to the processes preparatory for cell division. Also during this period the nutrition of the processes especially the axone would suffer, and finally, an equal division of a cell can occur only when the whole cell body with all its protoplasmic contents takes equal parts in the division, and this in the case of a nerve cell, is of course, impossible" (p. 108).

Since the evidence is convincing that the axone is the first of the branches to grow off from the cell-body, the appearance of mitotic figures in cell bodies that exhibit dendrites would be open to one of two explanations only. First, that the mitotic appearances are not necessarily followed by a division of the cell-body; or, second, that the cell-body does divide after the axone has been formed. If this latter were true, then we might expect to find two cells attached to a single axone. Those who have worked most with the methods which would show this relation if it existed, have not observed it. The first hypothesis therefore, appears the more probable.

Putting aside, as rare and atypical, the dividing nerve-cells which are multipolar cells and the spongioblasts, which perhaps should not have much stress laid upon them, there still remains



the large number of small and large cells which cannot possibly be classed together as undifferentiated descendants of the germinal cells, and which from the period of birth up to and possibly beyond the fourth day, form the majority of the cells concerned in the growth of the nervous system. That these cells are originally the offspring of the ventricular germinal cells of His seems most probable; that they have migrated into the outer layer by amoeboid movements there is every evidence to show, for not only are they found in the white matter, but some of them in both gray and white are fixed in shapes which suggest that they have been through amoeboid changes. They are not, however, simply germinal cells which have migrated away from the ventricles, for they differ from the germinal cells in the character of their cytoplasm and in their size. The largest ventricular germinal cells measure in the cord  $9 \times 12 \mu$ , the dividing cells of the gray matter up to  $12 \times 18 \mu$ .<sup>1</sup> The outline of the germinal cell is difficult to make out, the cytoplasm is clear, stains lightly; the outlines of the large dividing cells is distinct and the cytoplasm—the outer zone, at least—is granular and stains deeply with protoplasmic stains. Certainly these cells are not simply the germinal cells which have migrated from the ventricles, and if they are the offspring of the germinal cells, they have undergone some change before dividing for a second time; they have become at least partially differentiated. This will be seen more clearly if the dividing cells shown in the drawings from different regions be compared, those from the endyma, from the nerve fiber tracts and from the gray matter of the cord and the gray matter of the brain. If these cells are compared, it will readily be seen that in every instance the dividing cell tends to resemble in morphological character the resting cells in the region in which it is found. In the nerve fiber tracts the dividing cell is almost always small, narrow, with no apparent cell body—in other words it is like the neuroglia cell in these regions. Large dividing cells are rarely found in the fiber tracts, but in the cord

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<sup>1</sup> These measurements were not taken from the multipolar cells.

they occasionally are found near the edge of the gray matter, and in the brain, especially in the earlier stages, they may be found among the neuroblasts which are passing through the fiber tracts to the cortex. As for the large dividing cells which lie in the gray matter, they have an appreciable cell body, often quite as large as the nerve cells in those places, and it is noticeable that those found among the multipolar cells of the cord are as much larger than those in the cortex of the brain as the multipolar cells are larger than the pyramidal.

The obstacles to the assumption that fully formed nerve cells may divide are not only theoretical. Mitotic figures have been seen in the pyramidal cells of the cortex, in the neighborhood of an injury;<sup>1</sup> but under normal conditions, in vertebrates at least, the division of nerve cells has never been seen, and even in the cases cited above, it may be that the presence of mitotic figures is not a proof that the cells really were dividing, but simply that the nucleus had entered upon the preliminary stages of mitosis which would never have been completed. To the division of the neuroglia cells there are no such strong objections; indeed, if the theory of WEIGERT is accepted as to the dissociation of the glia fibers from the cells, there seems no reason why these cells should not divide.

Assuming, then, that the large dividing cells of the gray matter are not either indifferent germinal cells, or fully differentiated nerve cells, what explanation remains? Might it be that they are not now in process of division but have already divided, and before the nucleus has returned to its resting condition, differentiation has proceeded and the cell is changing to a multipolar or a pyramidal cell? To this it must be objected that during mitosis all the energies of the cell are absorbed in this process and a further differentiation never, so far as we know, takes place until this is completed.

It seems impossible to explain the different varieties of dividing cells in this animal except by assuming a process of

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<sup>1</sup> CATTANI (16), MONDINO (17), FRIEDMAN (18), COEN (19), MARINESCO (20), SANARELLI (21), VITZOU (22), TEDESCHI (23).

cell multiplication for the later stages of development which is different from that of the earlier. In the earlier stages, we find ventricular germinal cells dividing and their offspring gradually transformed to neuroblasts and supporting cells. In the later stages this process is replaced by the repeated division of immature neuroglia cells and immature nerve cells, which are undoubtedly specialized cells, but are not yet fully developed.

How long these cells retain their capacity for repeated division it is impossible to say, but apparently in the case of the white rat both kinds of cells continue to be capable of mitosis after the end of the 4th day of extra-uterine life.

### *Summary of Part II.*

1. There are at least two kinds of dividing cells in the central nervous system of the white rat; one small, with no visible cell-body, the other large with a well developed cell-body.
2. The neuroglia cells are derived from the small dividing cells; the nerve cells from the large ones.
3. The dividing cells found in the gray matter and fiber-tracts of the brain and cord, are not indifferent cells, but are partly differentiated, and by their size, character of cell-body and nucleus and predominant distribution, it is possible to tell which are to be nerve cells and which supporting cells.
4. Mitotic figures are occasionally found in multipolar nerve cells and in sporgioblasts.

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## DESCRIPTION OF FIGURES.

All the sections are from the white rat.

*Fig. 1.* Cross-section of lumbar cord of foetus (Body length 17 mm.), showing distribution of mitoses. Mitotic figures in black.

*Fig. 2.* Cross-section of lumbar cord of new-born rat, showing distribution of mitoses.

*Fig. 3.* Cross-section of cerebral hemisphere of foetus (Body length 17 mm.) showing distribution of mitoses.

*Fig. 4.* Cross-section of cerebral hemisphere of new-born rat, showing distribution of mitoses.

*Fig. 5.* Ependyma of foetal brain.

(a) Ventricular surfaces with germinal cells.

(b) Germinal cell at a distance from ventricle.

*Fig. 6.* Ependyma of lumbar cord of new-born rat.

(a) Typical germinal cells.

(b) Long pointed dividing cell in ventral plate.

*Fig. 7.* Ependyma of lumbar cord of foetus.

(a) Long dividing cell with process, in dorsal plate.

*Fig. 8.* Lumbar cord of new-born rat, anterior gray column.

(a) (b) dividing cells of 1st class, delicate chromosomes, no apparent cell body.

*Fig. 9.* Cervical cord of new-born rat, lateral fiber tracts.

(a) small dividing cell of 1st class.

*Fig. 10.* Brain of new-born rat, fiber tracts. Ventricular surface towards bottom of the figure.

(a) small dividing cell of 1st class.

(b) neuroblasts turning.

(c) neuroblasts which have finished their half revolution.

*Fig. 11.* Cervical cord of new-born rat, anterior gray column.

(a) small,

(b) large dividing cell of 2nd class, with thick chromosomes and granular cytoplasm.

*Fig. 12.* Cervical cord of new born rat, anterior gray column.

(a) large pointed dividing cell of the 2nd class.

(b) multipolar nerve cell.

*Fig. 13.* Lumbar cord of four days rat, anterior gray column.

(a) Spindle shaped dividing cell of 2nd class.

*Fig. 14.* Lumbar cord of new-born rat, posterior gray column.

(a) Large dividing cell of 2nd class in anaphase.

*Fig. 15.* Brain of foetus, cortical cell layer.

(a) pial surface.

(b) dividing cell of 2nd class.

*Fig. 16.* Brain of new-born rat, cortical cell layer.

(a) large dividing cell of 2nd class.

(b) pyramidal cell.

- Fig. 17.* Brain of four days rat, cortical cell layer.  
(a) large dividing cell of 2nd class.
- Fig. 18.* Cervical cord of new-born rat, anterior gray column.  
(a) multipolar cell with nucleus in prophase.
- Fig. 19.* Thoracic cord of new-born rat, anterior gray column.  
(a) multipolar cell with nucleus in prophase.
- Fig. 20.* Lumbar cord of new-born rat, anterior gray column.  
(a) multipolar cell with nucleus in prophase.

# THE MUSHROOM BODIES OF THE CRAYFISH AND THEIR HISTOLOGICAL ENVIRONMENT.

A STUDY IN COMPARATIVE NEUROLOGY.

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With Plates XXI—XXIV.

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## INTRODUCTION.

Mushroom-bodies, fungiform bodies, pedunculated bodies, are synonyms that have been applied to certain peculiar structures found in the brains of insects. These bodies were first discovered by DUJARDIN ('50). Although rediscovered by LEYDIG ('64) and RABL-RÜCKHARD ('75), yet aided by osmic acid, the microtome and staining fluids, DIETL ('76) was the first to give a complete description of the whole organ.

Thanks to the researches of more recent investigators, it is now well known that the mushroom-bodies occur in all classes of insects and that they reach their highest development in the Hymenoptera. DIETL ('76), BERGER ('78), and VIALLANES ('93) have found in the *Decapod* brain structures which they consider homologues of the mushroom-bodies of the *Hexapod* brain. KENYON ('96), as the following quotation shows, thinks all of these men are mistaken. "Special swellings found on the brains of certain of the Crustacea have been compared with them [the mushroom bodies], but it is to be seriously doubted, I think, whether such swellings or cellular heaps are properly to be homologized directly with them. In neither RETZIUS' figure of the brain of *Astacus fluviatilis*, nor in BETHE's figures of the brain of *Carcinus maenas*, can I find cells having the relations and the appearance of those I find in the bee. I have noticed nothing resembling the structures in isopods and amphipods, nor have I found indications of them in the brains of *Pauropus*, *Polyxenus*, juloid diplopods, *Scolopendrella*, *Lithobius*, nor even in several forms of *Thysanura* that I have examined. If cells homologous with those filling the cup-like calyx of the mushroom bodies of the bee are at all present in these forms, they are so undifferentiated as to be indistinguishable from the general mass of cells about them."

The purpose of this paper is to throw additional light upon this problem.

A portion of this work was done, during the summer of 1898, in the Hull Zoological Laboratory of the University of Chicago. I take this opportunity to express my indebtedness

to the authorities of that institution for the facilities and scholarship privileges granted me; and to Dr. E. L. PARKS and friends, whose cooperation made possible the spending of a summer in the above named institution. I am also under lasting obligations to Dr. W. M. WHEELER for suggestions and for the gift of some *Peripatus* material and for the loan of an extensive collection of insect slides. I must also express my thanks to Dr. C. M. CHILD, who kindly gave me well-fixed specimens of several polychæte annelids.

#### HISTORICAL.

After the historical accounts given by EMIL YUNG ('78), W. VIGNAL ('83), KRIEGER ('88), G. RETZIUS ('90), JULES RICHARD ('91), PAUL SAMASSA ('91), H. VIALLANES ('93), and C. H. TURNER ('96), an exhaustive résumé of the work already done on the crustacean brain would be out of place here. Any one interested the subject will do well to consult the works just mentioned. The papers of RETZIUS ('90) and VIALLANES ('93) are especially valuable for such a purpose. Throughout the text references will be made to the views of the various authors, and, at the end of this article, will be found a bibliography of the works on the central nervous system of the *Crustacea*. In this place it is proposed to epitomize the conclusions of only a few of the authors who have discussed it.

EMIL YUNG ('78) studied the nervous system of *Homarus*, *Palemon*, *Astacus*, *Cancer*, *Portunus*, and *Maia*. A portion of the paper is bibliographical and physiological; in the remainder of the paper the author comes to the following morphological conclusions:

1. The brain gives origin to the following seven pairs of nerves: the nerve to the frontal organ, the optic nerves, the oculomotor nerves, the antennulary nerves, the antennary nerves, the tegumentary nerves, and the nerves to the muscles of the antennules.

2. The nervous system of the decapod crustacea has the same elementary composition as the vertebrate nervous system; i. e., nerve fibers and nerve cells.

3. The nerve fibers occur in the peripheral nerves, the transverse commissures and longitudinal columns.

4. Each nerve fiber is provided with a sheath, which, in large tubes, is double.

5. The contents of the nerve tube is semi-viscous, clear and homogeneous.

6. The nerve cells which occur in all ganglia are of the following shapes: oval, pyriform, fusiform. In structure they resemble the cells of the sympathetic ganglia of vertebrates.

7. The cells are usually superficial.

8. Each ganglion contains three commissures.

9. There is no central body; what is considered such by authors is a collection of three transverse commissures.

10. The ganglia of the brains of *Brachyura* and *Macroura* are morphologically similar to each other and to the insect brain.

W. VIGNAL ('83) after giving an exhaustive historical résumé discusses the nervous systems of the Crustacea, Hirudinians, Oligochætes, and Mollusca. The following conclusions concerning the nervous system of the Crustacea were the fruits of his investigations of the following types: lobster, rock-lobster, *Palæmon*, crayfish and crab.

1. The membrane of the large nerve tubes has a double contour while that of the smaller a single. Otherwise they are similar.

The majority of the cells are unipolar, some are bipolar, still fewer are multipolar; but none are apolar. He could not detect the concentric arrangement of granular fibrils around the nucleus which REMAK describes.

3. The cells of the cerebrum, thorax and abdomen are chiefly unipolar.

4. The nerve chain is surrounded by two envelopes.

5. The two halves of the chain are united by commissural fibers and numerous cells.

6. The nerve cells on the ventral side of a ganglion send their processes into the center of the same.

7. The central ganglia are composed of nerve fibers and the prolongations of nerve cells.

8. The nerves of the stomatogastric system have the same structure as those of the ventral chain.

The author does not give a detailed description of the supra-oesophageal ganglion.

K. RICHARD KRIEGER ('88) truly remarks that EHRENBERG, VALENTIN, HELMHOLTZ, REMAK, HANNOVER, WILL, HAECKEL and other early observers, studied the histological elements only and ignored their relationships. He gives an instructive topographical drawing of the brain. Ignoring those portions which have no direct bearing upon the subject under discussion, the paper contains the following conclusions:

1. The brain of the crayfish is composed of the following four portions: An anterior swelling, a posterior swelling and two lateral swellings. These names explain the location of the parts. The anterior swelling consists of three portions, a median anterior nidus of cells, below which come, in the order named, the paired anterior and posterior bundles of 'punktsubstance' of the anterior swelling. The lateral swelling also contains an anterior and posterior bundle of 'punktsubstance.' On both the inner (mesal) and outer (lateral) sides of the anterior bundle of 'punktsubstance' of each lateral swelling lies a nidus of cells. The posterior swelling likewise contains a pair of anterior and a pair of posterior bundles of 'punktsubstance.' Between the anterior bundles lies a median nidus of cells; and the lateral portion of each posterior bundle is partly covered by a nidus of cells.

2. The ganglion cells have no membranes.

3. Two prominent optic tracts, coming from what DIETL and BERGER consider the homologue of the mushroom bodies, form a chiasm where all the fibers decussate.

4. There is a prominent tract which passes from each lateral swelling to the optic nerve of the same side.

5. From the anterior swelling fibers pass to the inner nidus of the lateral swelling, the outer nidus of the same and to the antennules.

6. From the posterior swelling fibers pass to the outer and inner nidus of the lateral swellings, to the optic nerves and to the antennæ.

7. Unlike BERGER, he does not think that any fibers arise from the anterior nidus.

8. Did not succeed in tracing any tracts into the collar.

G. RETZIUS ('90) gives an exhaustive historical résumé and demonstrates beyond a doubt the value of methylen-blue as a stain for nerve fibrils.

JULES RICHARD ('91) after a careful study of the nervous systems of *Diaptomus* and *Cyclops*, arrived at the following conclusions :

1. The nervous system resembles that of marine copepods of the same family.

2. The whole central nervous system is enveloped in a delicate membrane.

3. Certain parts of the brain contain unipolar but no multipolar cells. He also finds bipolar cells.

He does not discuss either the central body or the mushroom bodies.

PAUL SAMASSA ('91) studied *Sida crystallina*, *Daphnia sima*, MULLER, *Bythotrephes longimanus*, LEYDIG and *Leptodora hyalina*, LILLJEBORG. All of his methylen-blue preparations were a failure, but osmic-acid preparations gave good results.

1. Among all the Cladocera the central nervous system consists of the following four parts; the optic ganglia, the brain, the oesophageal commissures and the ventral chain. The brain and optic ganglion lie in front of the oesophagus. In *Daphnia* the optic bodies are united to the brain by two stalks, but in *Sida* they are fused with the brain. In *Leptodora* the brain and optic ganglion lie immediately beneath the eye.

2. In *Sida* the ventral chain consists of two longitudinal strands which are united by nine transverse commissures; but in *Leptodora* the ventral chain is fused into one mass.

3. The brain of *Sida* is composed of two pear-shaped masses, the 'punksubstanz' of which has the shape of the letter H, resembling in this respect the grey substance of the myelon.

4. A central body is found in the brains of *Sida*, *Daphnia*, *Bythotrephes* and *Leptodora*, but in no case did the author observe any fibers entering or leaving the body.

5. In *Sida* the nerves to the second antenna arise from ganglia in the collar, which ganglia are connected by a commissure.

6. In *Sida*, the oesophageal commissures terminate in the mandibular ganglion.

7. The maxillary ganglion is located in the collar, but has no commissure.

6. In *Sida* there are six pairs of feet ganglia and one pair of dorsal ganglia [*Stenerborsten-ganglien*] each having a commissure.

The paper also contains a résumé of the work done on the nervous system of the *Cladocera*.

H. VIALLANES' ('93) contribution is of such value that it is thought wise to give a résumé of his conclusions concerning not only the *Crustacea* but all the *Arthropoda*.

*General Remarks on the Organization of the Nervous System of the Articulates.* There are two types of nerve cells; ganglionic and chromatic. The chromatic have very little protoplasm. The nerves are formed of axis cylinders which react chemically in the same manner as nerve cells.

The nervous centers are composed of neuroglia, axis-cylinders and nerve cells. There are three types of axis-cylinders; centrifugal, centripetal and intrinsic. The centrifugal fibers, which are of about equal diameter throughout, arise from the large ganglion cells and constitute the motor fibers of the nerves. Along their course they give off lateral ramifying branches. The centripetal fibers are sensory. On entering the nerve center they ramify into finer and finer branches, but are not attached to the nerve cells. The intrinsic axis cylinders are ramifying fibers which arise from small cells which are situated in the ganglionic centers.

The nervous system begins as two longitudinal thickenings of the ectoderm which occur on each side of the meson. These thickenings fuse in front of the mouth to form the brain and

back of it to form the ventral chain. At first it is composed of a superficial and a deeper ganglionic layer. The cells of the ganglionic layer, by fusion, form the nerve cells. From the inner surface of the nerve cells ramify fibers forming the fibrillar substance. In the embryonic chain, each neuromere is lodged in a separate somite, the transverse commissures are large and double and the narrow longitudinal connectives are completely surrounded by ganglion cells.

In the adult the morphology of the ventral chain varies considerably in different types. In some cases the longitudinal commissures are long, but in others the ganglia are crowded together and lie in front of the somites innervated. An elongated nervous system does not represent a primitive condition, for in the embryo the longitudinal connectives are quite short. The compact chain does not represent so much a primitive stage as a stage in which the longitudinal commissures of the embryo have been effectually shortened.

*Brain of Insects.* The brain of the insects, which lies in front of and above the oesophagus, is composed of a protocerebrum, a deutocerebrum and a tritocerebrum—three neuromeres which correspond to three primitive somites.

The protocerebrum is composed of a median portion and two lateral optic ganglia. These optic ganglia, which are situated between the compound eyes and the median portion of the protocerebrum, are composed of three ganglionic masses. The median portion of the protocerebrum is composed of two lobes intimately connected at the meson. It contains: the mushroom bodies, the central body and the protocerebral bridge.

The mushroom bodies are united by commissural fibers to each other, to the optic ganglia of the same side, to the central body and to the olfactory lobes.

The central body, which is composed of fibers, has fiber connections with the cerebral lobes, the mushroom bodies, the optic ganglia and the olfactory lobes.

The deutocerebrum is composed of two hemispherical olfactory lobes. In addition to being united to its fellow by a

commissure, each olfactory lobe has fiber connection with the central body, the protocerebral and tritocerebral lobes of the same side.

The optico-olfactory chiasma connects the olfactory lobes with the optic lobe and mushroom bodies of the same side and with the olfactory lobe of the other side.

The tritocerebrum corresponds to the oesophageal ganglia of the crustacea.

The anatomical modifications seen in different species are determined by the following factors: the kind of food, the perfection of the senses, and the perfection of the psychic faculties. In forms that feed on solid food the oesophagus is large and the oesophageal commissures elongated, but in forms that feed on liquid food, the oesophagus is narrow and the oesophageal commissures correspondingly short. The size of the sensory lobes varies with the perfection of the sense organs; but the development of the mushroom bodies fluctuates with the psychic activities.

In the embryo, the three primitive folds develop into five: the first and second form the optic lobes; the third, the protocerebral lobes, the central and mushroom bodies, the fourth, the deutocerebrum, and the fifth the tritocerebrum.

*Brain of Myriopods and Peripatus.* Although constructed on the same plan, yet the brains of these forms are not so highly developed as those of insects. According to SAINT-REMY the brain of *Peripatus* is rigorously similar to the brain of insects and myriopods. From the standpoint of brain structure, the insects, the myriopods and onychophores constitute a close group.

*Brain of Crustacea.* Like the above forms, the brain consists of a protocerebrum, a deutocerebrum, and a tritocerebrum.

The protocerebrum is in all respects comparable to the protocerebrum of insects; but in many crustacea the optic lobes are not fused with the protocerebral lobes.

The mushroom bodies present the same aspect, the same structure and the same fibrous connections as in the insects. They are probably not psychic but optic in function.



The tritocerebrum, which gives nerves to the second antenna, is composed of a pair of oesophageal ganglia, rigorously comparable to the oesophageal ganglia of the insects and of a pair of nervous masses, the antennary lobes, intercalated between them. From the ventral surface arise the antennary nerve and from the dorsal the tegumentary nerve and the nerve to the eye stalk. The antennary lobes are united, not by commissures, but by a band of 'punktsubstance.'

Thus from the standpoint of brain structure the insects, myriopods and peripatus form a homologous group.

*The Brain of Limulus and Arachnids.* The brain is composed of only two segments: the protocerebrum and the deutocerebrum.

The protocerebrum is rigorously similar to that of the insects. In *Limulus* the mushroom bodies are enormously developed.

Among the crustacea, myriopods and insects, the deutocerebrum is pre-oesophageal and innervates the first antennæ. In *Limulus* and *Arachnids* it is also pre-oesophageal, but innervates the chelicera. There are no olfactory lobes and the tritocerebrum is absent.

In the following table VIALLANES has summarized some of his conclusions.

	Crustacea	Insecta and Myriopoda	Arachnida and Limulus	
1st somite —— Protocerebrum	Optic and psychic centers Innervates the eyes	Optic and psychic centers Innervates the eyes	Optic and psychic centers Innervates the eyes	Centers connected by the pre-oesophageal commissures
2nd somite —— Deutocerebrum	Olfactory center Innervates the 1st antennae Gives a root to the visceral system	Olfactory center Innervates the 1st antennae Gives a root to the visceral system	Tactile center Innervates the cheliceres and rostrum Gives a root to the visceral system	
3rd somite —— Tritocerebrum	Antennary lobe Tactile center Innervates the 2nd antennae Oesophageal ganglia Gustatory center Innervates the lips Gives a root to the visceral ganglia	Absent  Oesophageal ganglia Innervates the lips Gives a root to the visceral ganglia	Absent  Absent	
4th somite —— 1st post-oesophageal ganglion	Innervates the mandibles	Innervates the mandibles	Innervates the mandibles and 1st pair of maxillae	
				Centers connected by post-oesophageal commissures
				Brain

C. H. TURNER ('96) discusses the gross morphology of central and peripheral nervous system, but does not discuss the histology of the former. The following is a recapitulation of that paper.

1. The nervous system of *Cypris* consists of a supra-oesophageal ganglion connected to a ventral chain by a pharyngeal collar.

2. The ventral chain consists of a sub-oesophageal ganglion, which has probably been compounded out of at least three ganglia, and two subsequent ganglia.

3. From the supra-oesophageal ganglion arise a median unpaired optic nerve and paired antennular and antennary nerves. The antennary nerve, which arises from the place of union of supra-oesophageal ganglion and collar, receives a portion of its fibers from the collar.

4. From the sub-oesophageal ganglion arise the following

four pairs of nerves: labial, mandibular, labral, first maxillary and thoracic. The thoracic arises from the dorsal surface, the others from the ventral.

5. The second maxillary nerve arises from the first ganglion back of the sub-oesophageal.

6. From the last thoracic ganglion arises an unpaired abdominal and two pairs of leg nerves.

7. There is a median compound triune eye situated near the dorsal surface. Each division of this eye is supplied with retinal cells and a lens. In most Cypridæ the optic nerve is a median unpaired nerve which splits in three branches, but in *Notodromas* there are three optic nerves.

8. Between the base of the antennæ and the upper lip there is a pair of pear-shaped sensory organs, which are probably simple eyes. This organ is innervated by a branch of the labial nerve.

9. Bordering the mouth there are three pairs of similar sense organs which are innervated by branches of the labial, mandibular and labral nerves. The paper also discusses various sensory setæ.

EDGAR J. ALLEN ('96) discusses at length the histological elements of the embryonic lobster and arrives the following conclusions:

The thoracic ganglia are fused into one mass.

A nerve cell with all its branches constitutes a unit. [This unit is called by many authors a neurone.]

There are three main classes of neurones in the embryonic lobster brain: 1st, where all of the neurone lies within the central nervous system; 2nd, where the ganglion cell lies within the central nervous system and the fibers pass to the periphery; 3rd, where the ganglion cell lies in the periphery and the fibers penetrate into the central nervous system.

Class 1, which is composed of coordinating elements, is subdivided into four subclasses: A, where the fiber extends posteriorly (caudad) from the ganglion cell to the end of the ganglionic chain; B, where the fiber runs anteriorly (cephalad) from the ganglion cell to the brain; C, where the fiber runs

posteriorly (caudad) from the ganglion cell and terminates in the next ganglion; D, where the fiber passes anteriorly (cephalad) from the ganglion cell, giving off branches to the next ganglion and terminating in the next but one. A may either decussate or not decussate, B decussates, but C and D never decussate.

Class 2, which is composed of motor elements, is composed of seven classes: E, fiber enters the lateral anterior root of the same side; F, fiber branches and enters the same root from a ventral cell; G, cell situated in the median mass, the fiber enters the anterior root without branching; H, cell lies in the median mass, the fiber branches, then enters the anterior root; I, cell is situated in the median mass, the fiber branches and enters the posterior root; K, cell is situated in the median mass, the fiber decussates and enters the posterior root; L, cell lies near the median mass, the fiber enters the anterior root.

The elements of class 3 are sensory. On entering the ganglion each fiber split forming a Y, one branch of which passes forward (cephalad) and the other backwards.

Since frequent comparisons will be made with the annelid brain, it is thought wise to give the following few résumés.

EDWIN S. GOODRICH ('97) in comparing the Arthropod and Annelid head reached the following conclusions:

The prostomium may be one of three things: (1) a modified or reduced segment, (2) an incipient segment growing on the anterior surface of the peristomium, (3) not a segment at all but a peculiar structure.

In the development of Arthropods, new segments are invariably added between the last segment, the telson, and the one immediately in front of it. All apparent exceptions to this law of MILNE-EDWARDS seem to be due to retardation of development.

Careful modern researches show that in the *Oligochaetes* the peristomium exhibits the essential characters of a true segment. It is developed around the mouth and contains: (1) a mesoblastic somite, which becomes hollowed out to form a coelom; (2) a pair of ventral ganglia, which fuse with the suc-

ceeding segmental ganglia ; and (3) also a nephridium or head kidney. In *Polychætes* the cœlom of the peristomium is often obscure. In some cases a pair of somites are formed in the peristomium, which, becoming hollowed out, may even give rise to peritoneal funnels. In the *Polychætes* nephridia are usually developed.

The prostomium presents none of the characters of a true segment. It neither surrounds the alimentary canal nor contains a pair of mesoblastic somites nor develops within itself nephridia. Although finally becoming united with the cœlom, the cavity of the prostomium is primitively a blood-space and is cœlomic only by virtue of its connections. From one or more centers situated in the upper surface of this prostomium is developed the supra-oesophageal ganglion.

This prostomium is neither a vestigial nor an incipient metamere ; it is either a remnant of the region lying in front of the mouth of the primitive unsegmented ancestor of the worms, or else an outgrowth from the peristomium.

Since the region in front of the mouth in Arthropods is the fused product of several somites, the mouth has probably migrated backwards (caudad).

In *Peripatus*, where the head is composed of three segments, all agree that the two posterior (caudal) ones are true metameres, but some doubt exists as to the nature of the pre-oral, eye-bearing, segment. The researches of VON KENNEL and SEDGWICK which show that in its development, this segment resembles a true metamere, and the researches of KORSCHOLT and HEIDER, which indicate that the antennæ of *Peripatus* were originally post-oral, demonstrate that this first segment of *Peripatus* is a true metamere. The prostomium of *Peripatus* is insignificant ; the antennæ arise from the first segment.

The morphology of the myriopod head is imperfectly known, but it seems to resemble *Peripatus*.

In the *Hexapoda*, where the head is composed of six regions, three posterior (caudal) regions, belonging to the labium, maxillæ and mandibles, are universally considered true metameres. Counting from behind forwards, in the adult, the next

segment becomes reduced and disappears. The next but one, which bears the antennæ, is regarded by most writers as a metamere of post-oral origin. Concerning the remaining segment, there are three distinct views extant: 1, it represents the prostomium of the annelids; 2, it is merely a specialized anterior region of the antennal segment, which has been caused by a secondary subdivision; 3, it is a true metamere. The third view seems the most probable. It seems that, in the Hexapoda, the prostomium and archicerebrum have not been plainly distinguished.

In the *Arachnida*, where the head appears to be composed of two segments, the cheliceral and the procephalic, the cheliceral segment is undoubtedly a true metamere; but the procephalic segment offers the same difficulties of interpretation as does the most anterior (cephalic) segment of the insect head. It is probably a metamere.

In the *Crustacea*, where the head is composed of six segments, the last three are obviously true metameres; the next two are evidently post-oral metameres that have become pre-oral; as to the next there is much uncertainty.

Although much evidence is needed to substantiate the view, yet it seems quite likely that, throughout the Arthropoda, the procephalic lobes of the head are homologous and represent the peristomial segment of the annelids.

The following table, which has been copied from the paper of Dr. GOODRICH gives his views in a nutshell.

Annelida	Peripatoidea	Insecta	Arachnida	Crustacea
Prostomium with or without tentacles	?	?	?	?
Archicerebrum	Frontal processes			Frontal processes
Segment I or Peristomium	Procephalic lobes, antennæ, protocerebrum	Procephalic lobes, protocerebrum	Procephalic lobes, protocerebrum	Procephalic lobes, protocerebrum
Segment II	Mandibles, deutocerebrum	Antennæ, deutocerebrum	Chelicerae, deutocerebrum	1st antennæ, deutocerebrum
Segment III	Oral papilla	Rudimentary appendage, tritocerebrum	Trunk segment	2nd antennæ, tritocerebrum
Segment IV	Trunk segment	Mandibles	Trunk segment	Mandibles
Segment V	Trunk segment	1st maxillæ	Trunk segment	1st maxillæ
Segment VI	Trunk segment	2nd maxillæ	Trunk segment	2nd maxillæ

J. J. HAMAKER ('98) has studied exhaustively the nervous system of *Nereis*. The results of his research may be epitomized as follows :

Throughout the ventral cord is differentiated into ganglia.

The brain gives origin to the following fourteen pairs of nerves: I, nerve to the proboscis; II, nerve to the antenna; III, nerve to the dorsal wall of the head; IV, nerve to the palp; V, nerve to the ventral side of the proboscis; VI, sensory nerve to the palp; VII, nerve to the palp; VIII, IX, X, roots of the oesophageal commissure; XI, XII, optic nerves; XIII, nerve to the ciliated groove; XIV, nerve to the dorsal surface of head. In addition to these fourteen pairs of nerves there is a median unpaired nerve which passes to the dorsal surface of the head.

In the oesophageal collar there is a ganglion which sends nerves to the anterior cirrus, to the proboscis and also a branch which, passing forward (cephalad), unites with V to form a ganglion.

The sub-oesophageal ganglion gives rise to three pairs of nerves and each other ventral ganglion gives origin to five pairs of large and several smaller nerves.

The parapodia are innervated almost entirely by the parapodial ganglion, from which four nerves radiate towards the periphery.

The following cell nidi are found in the supra-oesophageal ganglion: 1, in front, on each side of the brain, between the anterior median and the anterior lateral groups of nerves, there exists a large ventral and a smaller dorsal group of small cells arranged in radiating rows; 2, on the posterior border there is a group of spindle-shaped cells with indefinite boundaries; 3, along the inner border of 2 there is a group of pear-shaped cells with definite cell-membranes; 4, near the meson there is a group of pear-shaped cells; 5, at the side of the brain, beneath the anterior eye nerve, there is included in the brain a group of cells which seem to have no other connection with the brain; 6, other large cells.

The central nervous system of *Nereis virens* occupies a

deeper position than does the nervous system of most *Polychaeta*. It is separated from the hypodermis by the circular muscles and is enveloped by an elaborate protective tissue.

The protective tissue is of two kinds: an inner spongy layer, the neuroglia, which is of ectodermal origin, and the neurilemma, which is mesodermal in origin.

The mushroom bodies of insects and decapod crustacea are represented in the brain of *Nereis* by the anterior masses of small nuclei.

In some species of *Nereis* the optic ganglion lies beneath the anterior eye, in others it lies within the brain capsule.

There is no neuropil in the nerve cord.

There is one small median and two larger lateral connectives between each two successive ganglia of the ventral nerve cord.

The sheaths of the nerve fibers have no nuclei; hence they must be a product of the fibers themselves.

The nerve cells of the ventral cord commonly have one or more centrosomes.

The giant fibers are nervous in function and are connected to the periphery by ordinary centrifugal fibers. The giant fibers do not give off fibrillations, and nervous relation with other fibers is established directly between the axis cylinders.

Where certain decussating fibers cross, their axis cylinders are united by anastomoses.

The ends of certain centripetal fibers of the same set are always united by anastomoses.

Contact between their axis-cylinders may possibly be one of the means of bringing nerve fibers into functional relation with each other.

#### MATERIAL.

In this study the following material has been used: the common crayfish (*Cambarus* sp?), *Limulus*, *Branchipus*, *Gammarus*, *Nereis*, *Polynöe*, *Lepidonotus*, and the common earth worm.



## METHODS.

Several methods were tried but the best results were obtained with Mallory's hæmatoxylin and the methylen-blue method. In the first case the brains were fixed in 10% formaldehyde. Before staining the sections were mordanted in about a 5% aqueous solution of copper sulphate for from 12 to 24 hrs. In the second case the fresh brains were stained in a weak solution of methylen-blue. The brains were kept on ice while being stained, washed and hardened. They were fixed in the usual way and mounted whole or sectioned. After many failures a few good specimens were secured. Unfortunately all my notes on the method have been lost and details cannot be given.

## GENERAL TOPOGRAPHY.

There are sufficient physiological reasons to justify KENYON ('96) in including under the general term brain "the whole of the neural mass included within the head, excepting only the small ganglia known as the stomatogastric ganglia;" but throughout this paper the word is used in quite a different sense. In these studies the word brain is restricted to that nervous mass which is composed of the protocerebrum, deutocerebrum and tritocerebrum. It will be seen at once that what is here called brain has been termed by KENYON, the dorso-cerebrum, and by others the supra-oesophageal ganglion.

Viewed from its cephalic aspect the brain (supra-oesophageal ganglion) of *Cambarus* is sub-rectangular in outline. The dorsal and ventral sides of this rectangle are slightly concave, but the lateral boundaries are strongly convex (fig. 1). From right to left the brain is about twice as long as it is from above downwards (dorso-ventrally); but from before backwards (cephalo-caudal) the diameter is shorter still.

The decapod brain is quite compact and resembles in many respects the supra-oesophageal ganglia of insects. There are, however, two points of contrast that are quite conspicuous. In the first place, in the Insecta, a pair of optic nerves are fused with the brain; but in the Decapoda the optic ganglia are lo-

cated in the eye-stalk and connected to the brain by what is known as the optic nerve. Again, in the insects, tracheæ surround and even penetrate the brain; but, in the decapod crustacea, there are no tracheæ to complicate matters. These two minor points of difference do not militate against the idea that the brains of insects and crustacea are homologous organs.

It has been demonstrated by VIALLANES ('93) and others that the brain of the crayfish, like that of the insects, is composed of the following three regions: protocerebrum, deutocerebrum, tritocerebrum. Although agreeing in this matter with VIALLANES, and occasionally referring to each of these regions as such, yet the author does not propose to bound accurately these regions, for the simple reason that in the adult there are no sharp demarcation lines between these segments and any attempt to locate absolute boundaries is sure to be, not only artificial, but also confusing.

Viewed from its cephalic aspect, the brain of the crayfish (*Cambarus*) is composed of a median portion and two lateral swellings. This median portion easily differentiates itself into a dorsal and a ventral region.<sup>1</sup> The lateral swellings contain the mushroom bodies and the optic and olfactory lobes (fig. 1, *Ol. L.*, *Op. L.*).

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<sup>1</sup> Students of invertebrate neurology will recall that KRIEGER ('88) divides the median portion of the crayfish brain into anterior and posterior swellings. What KRIEGER has called anterior is here called dorsal and what KRIEGER has called posterior is here called ventral. The reason for this change in nomenclature will now be given. The brain of the decapod crustacea is so located in the head that that portion from which the optic nerve arises is directed upwards (dorsad), while the portion from which the antennular nerve arises is directed forwards (cephalad). This may be easily demonstrated, either by dissections of *Cambarus* or by transverse sections through the entire head of *Palemon*. On viewing a brain that has been removed from the body of a decapod, one is inclined to call that portion from which the optic nerve springs the cephalic end. I was misled until, on examining some sections through the entire head of *Palemon*, I found that the dorsal portion of the brain of *Palemon* agreed in all essentials with what I, along with others, had been calling the cephalic end of the brain of *Cambarus*. This led to a careful examination of the *Cambarus* brain *in situ*. Then I discovered that the optic nerve arises from the upper (dorsal) portion of the brain.

## CEREBRAL NERVES.

The crayfish brain, as here defined, gives rise to the following five pairs of nerves: optic nerves, oculo-motor nerves, antennular nerves, tegumentary nerves and antennary nerves.

*Optic nerves* (fig. 1, *O.N.*). These constitute a pair of large nerves which pass from the brain to the optic ganglia. One arises from each dorso-lateral corner of the brain and passes upwards and outwards (dorso-laterad) to the optic lobe.

The nerve does not exist in the insects, but its homologue is found within the hexapod brain.

This nerve is composed of the extra-ganglionic portions of the fiber tracts that lead from several ganglionic centers to the optic ganglia. In the Hexapoda the optic ganglia are a part of the brain, hence there is no extra-ganglionic portion of these optic tracts. In those insects that have eyes situated at a greater or less distance from the brain there is a nerve, known as the optic nerve, which passes from the optic ganglion to the eye. But this is quite a different structure from the optic nerve of those Decapoda whose optic ganglia are situated within the eyestalks.

It must not be hastily concluded that in all Crustacea there is an extra-ganglionic portion of the optic tracts, known as the optic nerve, which passes from the brain to the optic ganglion, which is situated either in the eyestalk or near the eye. In *Gammarus*, an amphipod, the eye is sessile on the brain and this nerve is absent. Nor would one be warranted in stating that in the higher *Crustacea* we have invariably an optic nerve of the type found in *Cambarus*, while in the lower forms the nerve is always absent; for in the phyllopod *Branchipus*, a form much lower in the scale than *Gammarus* my preparations show quite a long optic nerve connecting the brain to the eyes. Even in closely allied forms the relation of brain to optic ganglion is not the same; for according to SAMASSA ('91), in *Sida crystallina*, a cladoceran, the optic ganglion is fused with the brain, while in *Daphnia sima*, O. F. MULLER, another cladoceran, the optic ganglion is united to the brain by two stalks.

Among the fresh water *Ostracoda*, the optic nerve is, ex-

cepting in *Notodromas*, a median unpaired structure. Where it leaves the brain there is a cluster of cells. Whether or no these cells are the homologue of the optic ganglion of the higher forms is an unsettled point. If not, then the optic ganglion is absent. In my paper on the nervous system of *Cypris* ('96) I unfortunately called that the optic ganglion and described the optic nerve as arising from it. But in so doing it was not intended to predicate the homology of that group of cells with the optic ganglion of insects. The nomenclature was unhappy. Optic nidus would have been a better expression.

*Oculomotor nerves.* Near the latero-ventral edge of the brain of *Cambarus* arises a nerve which passes to the eye muscles (fig. 1, *O.M.N.*). This nerve is not found in the *Hexapoda*. There sessile eyes render it unnecessary.

In *Branchipus*, from a theoretical standpoint, I expected to find this nerve, but if it exists, I have not been able to differentiate it from the optic nerve.

*Antennular nerves.* From near the middle of the cephalic surface of the brain arise the antennular nerves. They pass forward (cephalad) to the antennules (fig. 1, *A.N.*).

This nerve is also found in the *Cladocera* (SAMASSA, '91), the *Ostracoda*, and the *Hexapoda* (VIALLANES, '93 etc.).

*Tegumentary nerves.* This nerve arises from the caudal surface of the brain, near the origin of the oesophageal collar and passes latero-cephalad to the skin of the head (fig. 1, *T.N.*).

It has not been possible to determine whether this nerve is found in the insects or not, but I feel quite sure that it is not homologous with the tegumentary nerve of the *Ostracoda*.

*Antennary nerves.* This is a large pair of nerves which arise from each ventro-lateral edge of the brain and pass outwards (laterad) to the antenna (fig. 1, *Ant.*). Immediately after leaving the brain, a small nerve arises from the antennary nerve and passes downwards (ventrad).

This nerve (the antennary) seems to be universally present throughout the *Crustacea*; but according to VIALLANES ('93) and other students of insect neurology it is found neither in the *Hexapoda*, nor the *Arachnida*, nor the *Myriapoda*, nor *Limulus*.

Although the above enumeration of nerves agrees perfectly with KRIEGER ('88), yet students of invertebrate neurology will notice at once that it does not tally with YUNG ('78) who describes seven pairs of cranial nerves. One of the nerves mentioned by YUNG which is not included here is the nerve to the frontal organ. Although occasionally I have thought that I detected a small nerve passing from the front of the brain to the rostrum, yet I have not been able to demonstrate, to my own satisfaction, the existence of such a nerve. The other nerve not included here is the antennulo-motor nerve. Although it stands to reason that there must be an antennulo-motor nerve, yet I have not been able to differentiate it from the main antennular nerve. The following comparative table will emphasize this point.

CRANIAL NERVES OF THE DECAPODS.

Yung	Krieger	This paper
To frontal organ	—	?
Optic	Optic	Optic
Oculomotor	To eye muscles	Oculomotor
To antennules	1st antennary	Antennulary
To muscles of the antennules		
Tegumentary	Tegumentary	Tegumentary
To the antenna	2nd antennary	Antennary

In this paper it is not thought wise to attempt to point out homologies between the cerebral nerves of the crayfish and those of the *Annelida*.

## CELL NIDI.

In the Décapod brain, the following eight clusters of nerve cells are easily recognized: an unpaired dorsal nidus, a pair of inner mushroom nidi, a pair of outer mushroom nidi, a pair of latero ventral nidi, and an unpaired ventral nidus. In addition to these cell clusters, neuroglia cells are scattered throughout the brain. In some regions the cells are collected in clusters.

This is especially so along the median line, where in some places they form chains uniting the dorsal and ventral nidi.

Although this paper recognizes the same number of nidi in the brain as does KRIEGER ('88), yet the names given by him are not retained here, because some are misleading and others are cumbersome to handle. For instance what he calls the anterior nidus is on the dorsal surface of the brain and what he calls the posterior nidus is on the ventral side of the brain. "Outer nidus of the lateral swellings" is certainly cumbersome to handle.

Below is tabulated the names used by KRIEGER and the terms proposed and used in this paper :

CELL NIDI OF THE DECAPOD BRAIN.

KRIEGER'S names	This paper's names
Anterior cell nidus (unpaired)	Dorsal nidus (unpaired)
Inner nidus of the lateral swellings (paired)	Inner mushroom nidus (paired)
Outer nidus of the lateral swellings (paired)	Outer mushroom nidus (paired)
Outer nidus of the posterior swellings (paired)	Latero-ventral nidus (paired)
Posterior nidus (unpaired)	Ventral nidus (paired)

*Dorsal Nidus* (figs. 1-3, 7-9, 17, 18, *D.N.*). This is a large cluster of cells which extends over most of the dorsal (figs. 1-3, 5, 7-9) and a large portion of the cephalic (figs. 15, 17, 18) regions of the brain. The principal cells of this nidus are large and contain large nuclei and small nucleoli. Among these cells numerous neuroglia cells are distributed (fig. 32).

On the dorsal surface of the brain of *Nereis* there is a cluster of pear-shaped cells which may be the homologue of this nidus.

*Outer and Inner Mushroom Nidi* (fig. 1, *O.M.N.*, *I.M.N.*). These cell clusters resemble each other and differ from all others in having their cells arranged in rows which radiate from a common curve (fig. 23). They will be described in full in connection with the mushroom bodies.

*Latero-ventral Nidus* (fig. 1, 5, *L.V.N.*). This is a small cluster of cells which occurs on the caudal aspect of the latero-ventral portion of the brain. It covers the caudal portion of the antennary nerve. The cells of this cluster resemble those of the dorsal nidus.

*Ventral Nidus* (figs. 1, 2, 17, *V.N.*). This is a cluster of cells occupying the cephalic portion of the ventral side of the brain. Histologically it resembles the dorsal and latero-ventral nidi. On the cephalic aspect of the brain the dorsal and ventral nidi practically more or less unite, by means of neuroglia cells.

#### LOBES OF FIBRILLAR SUBSTANCE.

The histological groundwork of the Decapod brain is composed of a meshwork of fine fibrils which has been variously called "Punktsubstanz" (LEYDIG), "Marksubstanz" (DIETL), "fibrillar substance" (KENYON), etc. This fibrillar meshwork is segregated into more or less distinct fibrillar structures. In this paper these separate clusters of fibrillar substance are called lobes.

This paper recognizes eight paired and two unpaired lobes which are of sufficient importance to deserve mention. Six of these paired lobes and the two unpaired lobes are situated in the median portion of the brain; while the remaining two paired lobes are located in the lateral swellings. In the median portion are found the following lobes: dorsal lobe, inferior dorsal lobe, antennular lobe, tegumentary lobe, antennary lobe, pyriform lobe, the procerebral bridge and the central body. In the lateral swellings are found the optic and olfactory lobes. Even when all of these lobes have been located it will be seen that there is still a portion of the fibrillar substance left in which these various lobes are imbedded,

Most of these lobes have been described and located by KRIEGER ('88). The following table will show how the lobes here described correspond to those described by him.

KRIEGER	PRESENT PAPER
Anterior Punktsubstance of the anterior swelling	Dorsal lobe
Posterior Punktsubstance of the anterior swelling	Inferior dorsal lobe
Punktsubstance of the antennular nerve	Antennular lobe
Punktsubstance of the tegumentary nerve	Tegumentary lobe
Punktsubstance of the antennary nerve	Antennary lobe
?	Pyriform lobe
?	Procerebral bridge
?	Central body
Posterior Punktsubstance of the lateral swellings	Optic lobe
Anterior Punktsubstance of the lateral swellings	Olfactory lobe

*Dorsal Lobe.* All that portion of the median fibrillar mass which lies above (dorsad of) the central body is called the dorsal lobe (fig. 1, *D.L.*).

*Inferior Dorsal Lobe.* Immediately below (ventrad of) the central body there is another aggregation of fibrillar substance which is called the inferior dorsal lobe (fig. 1, *I.D.L.*). There is no sharp morphological demarcation between the dorsal and inferior dorsal lobes and I believe that they are physiologically similar.

*Antennular Lobe.* This is an ellipsoidal lobe which lies just inside (mesad) of the inner dorsal edge of the optic lobe. It is so called because it is formed in a great measure, of fibers from the antennular nerve (fig. 1, *A.L.*).

*Tegumentary Lobe.* This is a small, nearly spherical lobe, which is situated near the upper (dorsal) portion of the ventral nidus (fig. 1, *T.L.*). This bears the same relation to the tegumentary nerve that the antennular lobe does to the antennular nerve.

*Antennary Lobe.* This is a large ellipsoidal lobe lying in the ventral portion of the brain at the origin of the antennary nerve (fig. 1, *Ant. L.*).

*Pyriform Lobe.* This is a small but conspicuous lobe situated near the inner mushroom nidus (fig. 1, *P.L.*). This is best studied in longitudinal sections where it is seen lying above and



in front of (dorso-cephalad of) the optico-olfactory commissure. For a thorough understanding of the structure of this lobe a careful study of the series of sections shown in fig. 33 will be more instructive than any combination of words could possibly be.

*Central Body.* This peculiar structure seems to be found in the brains of all Arthropoda. LEYDIG discovered it in ants but mistook it for a part of the commissural system. To DIETL ('76) belongs the credit of recognizing it as a distinct structure. He called it the fan-shaped body (fächerförmig Gebilde). Later FLÖGEL called it the central body by which name the structure is now generally known.

VILLANES ('93) after having studied this structure in various insects, recognized it in the Crustacean brain; but other observers think that he is mistaken. YUNG ('78) after a careful review of the work done upon the Crustacean brain, declares that there is no such structure; but that there are three sets of transverse fibers which various men have taken for a central body. KRIEGER ('88) in his study of the crayfish brain must have overlooked this body, for I find no mention of it in his work. JULES RICHARD ('91) in his work on the nervous system of the Copepoda does not mention a central body; but SAMASSA ('91) in his studies of the Cladocera has found it in *Sida*, *Daphnia*, *Bythotrephes* and *Leptodora*.

In this study of the Crustacean brain I have been able to demonstrate the existence of a central body, not only in the crayfish (figs. 1, 8, 9, 17), but also in a form as low in the scale as *Branchipus* (fig. 34).

The structure of this body has puzzled more than one investigator. VILLANES ('91) asserts that it is connected by fibers to all parts of the brain. BERGER ('78) says that the body receives a bundle of fibers from each side, which fibers, on entering the body, break up into fine fibrils. KENYON ('96) thinks VILLANES' statement is too sweeping. He says the body is composed of fine fibrils many of which are derived from the branches of the commissure that passes by it. KENYON writes as follows: "Taken as a whole the fibers seem to reach it [central body] from nearly all directions but the two parts

seem to be supplied somewhat differently. Those entering the lower are seen to originate from cells above the antennal lobes and upon reaching the lower lateral edges to take a transverse course below the body and send several branches upwards that subdivide arborescently producing a compact mass of branchlets that recall the arborescent and bushy terminations of the association of fibers in the roots of the mushroom bodies. As in the case of these latter fibers, it is to the compact branching mass of fibrils that is due the depth of color so noticeable in preparations stained with osmic acid or haematoxylin. Other fibers pass out or enter from the fibrillar substance of the brain immediately in front, while branches from association fibers in the anterior region seem to enter the anterior end and the posterior lower end of this portion of the body." SAMASSA ('91) states that he has not been able to detect any fibers entering the central body.

Histologically considered, the central body of the crayfish is composed of a mass of fibrils and fibers free from any admixture of nucleated cells. In the immediate neighborhood, however, there are numerous neuroglia cells. The fibers composing this body seem to fall into two classes: 1st, numerous fibers forming a loose net-like meshwork which is continuous on all sides with the meshwork of fibers which seems to form the histological skeleton of the brain; 2nd, fibers which differentiate arborescently into numerous fine fibrils. The fibers of the second type are derived in part from the commissures which pass above (dorsad) and below (ventral of) the central body, in part from fibers that originate in the dorsal nidus and in part from cells lying in the immediate neighborhood of the central body. As to the first two sources of these fibrils my sections give abundant evidence; but the last statement is based upon the study of one slide. In one section I discovered a cell which gave rise to a fiber which forked, one branch passing into the central body and one passing towards the adjacent commissure (fig. 36).

Of the fibers which VIALLANES claims pass from this body to all parts of the brain I find no trace.

It would be claiming too much to hope that the above description entirely solves the structure of the central body. Other fibers may enter into its composition of which the sections studied give no clue, but it is thought that sufficient has been deciphered to show that the central body of the decapod crustacean brain is homologous to the central body of the insect brain.

Among the worms, in both *Lepidonotus* (fig. 30, *C.B.*) and in *Polynoe* (fig. 33, *C.B.*) is found a structure which, judging from its histological structure and its location, I take to be the homologue of the central body of the Crustacea and Insects.

*Procerebral Bridge.* In the crayfish this is a median fibrillar body which lies above (dorsad of) the central body (fig. 1, *P.B.*) and between the dorsal nidus and the median fibrillar mass. In both transverse and horizontal sections this body is horse-shoe shaped, with the horns directed towards the outside of the brain.<sup>1</sup> When viewed with a low power this seems to be an unpaired structure, but medium and high powers show that it is a paired structure; the two halves being connected by commissural strands (fig. 7, 8, *P.B.*).

Histologically the procerebral bridge resembles the central body in being composed of a meshwork of fine fibrils. In size however it is much smaller.

Both VIALLANES ('93) and KENYON ('96) express the belief that the branches and the nerves of the ocelli enter this body; but each admits that he has no conclusive proof of that assumption. Since this body is quite prominent in the Crustacea, where there are no ocelli, it seems conclusive that few if any of the fibrils of this body are derived from the nerves of the ocelli.

As to the source of the fibrils I have no conclusive evidence, but there is much that leads me to believe that they originate in the numerous cells that environ the procerebral bridge.

Both VIALLANES ('93) and KENYON ('96) state that, in the insects, fibers connect the procerebral bridge with the central

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<sup>1</sup> In one case out of many examined I found the horns directed inwards.

body. In the crayfish brain I have not been able to trace any fibers from the procerebral bridge to the central body; but numerous fibers arise in the dorsal nidus (which lies just above the procerebral bridge) and pass around the procerebral bridge to the central body and to the commissure which lies just above the central body. If these fibers give off branches to the procerebral bridge I have not been able to detect them.

Although the central body is present in *Branchipus*, yet my sections reveal no trace of the procerebral bridge; but since in that case one section contains the whole of the central body, the much smaller procerebral bridge might have been destroyed by the microtome knife. It would not be wise then to conclude that there is no procerebral bridge in *Branchipus*.

Most of my sections of worms reveal nothing that I would feel justified in calling a procerebral bridge; but in transverse sections of *Lepidonotus* I find a structure (fig. 30, *P.B.*) which may be the homologue of the procerebral bridge. In *Lepidonotus* this structure is composed of a meshwork of fibers which reacts towards stains in the same manner as the fibers of the procerebral bridge of the crayfish. Near it is a cluster of cells which may correspond to the dorsal nidus of the crayfish brain.

*Olfactory Lobe* (figs. 1-9, 14, 20, 25, *Ol.L.*) The olfactory lobes are located one in the dorsal portion of each half of the brain, between the outer and inner mushroom nidi. Each lobe is nearly spherical in shape and is about five millimeters in diameter. Histologically, the body is composed of three parts: 1st, a central core of fibers (fig. 5, *a*); 2nd, a region composed of fine fibrils arranged in dense subconical masses which radiate from the central core (fig. 5, *b*); 3rd, an outer layer of fibers (fig. 5, *c*).

*Optic Lobe* (fig. 1-9, 11-14, 20-23, 25, *Op.L.*). The optic lobes are located one in the ventral portion of each half of the brain, between the mushroom nidi and the latero-ventral nidus. They are ellipsoidal in shape and are much larger than the olfactory lobes. Histologically the body is composed of numerous fine fibrils grouped in such a manner as to cause sections of the body to have a mottled appearance. In the center of the dorsal lobe

enter fibers which will be described in connection with the fiber tracts of the brain.

#### FIBER TRACTS AND COMMISSURES.

*Fibers Related to the Optic Nerve.* The fibers related to the optic nerve may be classified as commissures and tracts. The commissures are two in number; the upper and lower optic commissures.

*Lower Optic Commissure* (fig. 8, 9, *Ia. Ib. Ic. Id.*) In *Cambarus* the presence of the lower optic commissure can be demonstrated by either the methylen-blue or the copper-sulphate haematoxylin method. In methylen-blue preparations a few fibers may be seen connecting the optic nerves; but in the copper-sulphate haematoxylin sections four bands of fibers connect the optic nerves (figs. 8, 9). All of these fibers lie in the same plane and are sub-parallel, forming downwardly directed convex curves. For convenience in reference, beginning at the upper end of the brain these tracts are designated "a," "b," "c," "d." Band "a," which lies immediately below the dorsal nidus, connects the dorsal portion of the optic nerve. Band "b," which lies about half way between band "a" and the central body, and "d," which lies immediately below the central body, connect the lower portions of the optic tracts. Bands "a," "b," "d" seem to be purely commissural, but into band "c" enter fibers which originate in its dorsal nidus. From band "c" fibers pass into the central body and in some cases it can be demonstrated that some of the fibers that enter the central body come from fibers which pass from the dorsal nidus to band "c" of this lower optic commissure. As has already been stated, some of the fibers of the central body are derived from band "d" of the lower optic commissure.

This lower optic commissure is found not only in the higher but also in the lower Crustacea, for I have found it in *Branchipus*, where it consists of three instead of four bands. In that case bands "a" and "b" seem to be fused.

KENYON ('96) recognized this in the bee brain and called it the lower optic commissure. Feeling sure that these commis-

tures are homologous in insects and Crustacea, I have retained his name although, in reality in the crayfish the lower optic commissure is, for the most part, higher than the upper optic commissure. In the bee brain KENYON found this commissure to be a much more compact structure than it is in *Cambarus*. This is in keeping with the fact that the insect brain is much more compact than the crustacean brain. In the insects the optic lobes are fused with the procerebrum, but in the crayfish, the optic lobes are apart from the brain, being connected to it by the optic nerve. This difference accounts for the compact arrangement of the lower optic commissure in the crayfish.

Thus it appears that the lower optic commissure exists in the lower as well as the higher Crustacea and that it is homologous to the lower optic commissure of the insects.

*Optic Chiasm or Upper Optic Commissure.* This commissure has long been known. To the best of my knowledge DIETL ('76) and BERGEN ('78) were the first to describe it. VIALLANES ('87) found it in *Oedipoda*, CUCCATI ('88) in *Somomyia*, KRIEGER ('88) in *Astacus* and KENYON ('96) in the bee. Although all of these authorities are describing the same organ, yet there is a diversity of opinion concerning it which is, to say the least, confusing.

DIETL and BERGER think there is a partial decussation of fibers in this commissure, while VIALLANES, KRIEGER and KENYON assert that there is a complete decussation.

In *Cambarus* this commissure is quite conspicuous. A careful study of several series shows that each of these investigators has stated a truth, but that no one of them has stated the whole truth. Associated with this chiasma in the crayfish there are three sets of fibers (fig. 2, *O.C.*). One set is purely commissural (fig. 2, 7, *O.C.*). This set occupies the upper portion of the chiasm. It is a concave band with its concavity directed upwards (dorsad). A second set decussates to the other side. A third band passes by in a convex curve without sending any fibers to the other side (fig. 7, *O.C.*). It will be seen that this commissure resembles very

much the optic chiasm of the vertebrates. I have not been able to identify this tract in *Branchipus*.

*Dorso-lateral Optic Tract.* This tract arises from the lateral portion of the dorsal nidus and passes in a ventrally directed convex curve (latero-ventrad) almost to the inner mushroom nidus; there it branches, a portion going to the outer tract of the optic nerve and the remainder passing downwards (ventrad) into the neighborhood of the stalks of the mushroom body where I lost it. There is much which leads me to believe that the forking of this tract is caused by each fiber dividing into two branches; but the evidence at hand is not conclusive (fig. 2, *D.L.*).

*Optico-mushroom Tract* (figs. 2, 5, 20, 23, *O.M.T.*). This is a prominent tract which may be readily traced from the inner (mesal) portion of the optic nerve to the optic chiasm (fig. 2, 7). There it branches, one branch decussating through the optic chiasm, the other making a sharp turn (fig. 7) and passing along with the decussating tract from the opposite side to the stalks of the mushroom bodies (fig. 2). There it branches, one branch passing into the optic lobe and one branch into the olfactory lobe (fig. 7, 20).

Fibers which originate in the outer mushroom nidus enter the optic lobe along with the fibers of the optico-mushroom tract. For a long time I was inclined to believe that the fibers arising from the outer mushroom nidus branched upon reaching the optic lobe, one fork passing into the lobe and the other passing into the optico-mushroom tract, but I have not been able to demonstrate this.

This optico-mushroom tract corresponds to one of the optic tracts described by KRIEGER ('88). In a figure he shows that the tract does not decussate through the optic chiasm, but terminates in the mushroom body of the same side.

*Optico-oesophageal Tract.* This is a small tract which passes from the inner portion of the optic nerve to the oesophageal collar of the same side.

Although a small tract, yet in methylen-blue preparations

I have been able to trace a single fiber from the nerve to the collar of the same side.

*Optico-arch Tract* (fig. 3, 5, *O.A.T.*) This is a small tract which passes from the medial portion of the optic nerve, in a convex curve (convexity mesad) to the fibrillar arch. Near the optic nerve this tract is intimately associated with the anterior optic tract, but, at the optico-olfactory commissure, this enters the arch, turns outwards (laterad) and passes along towards the mushroom bodies, while the anterior optic tract crosses the arch and passes on to the ventral nidus of the same side.

*Anterior Optic Tract* (fig. 5, *A.O.T.*). This is a small tract which passes from the optic nerve to near the root of the oesophageal collar and near the base of the antennary nerve. Where this tract apparently terminates there is a nidus of cells, but whether or not there is a direct union of those cells with the fibers of this tract could not be demonstrated. Between the optic nerve and the fibrillar arch this tract is intimately associated with the fibrillar arch tract; but near the arch they part company, this tract crossing the arch, the other curving into it.

I take this tract to be the homologue of what KENYON ('96) in the bee brain calls the anterior optic tract.

*Oculomotor Commissure.* Although there is a distinct oculomotor nerve yet, in sections, it is almost impossible to distinguish it from the optic nerve proper. In addition to the commissure described above, there is connected with the eye-nerves another commissure which in form resembles very much the lower optic commissure. Between it and the lower optic commissure are located the central body, the optic chiasm with its associated tracts, etc. Whether it belongs to the optic nerve proper or to the oculomotor nerve cannot be decided positively on account of the intimate relation to the two nerves. I am inclined to believe it related to the oculomotor nerve.

*Oculomotor Tract.* This fiber tract arises near the tegumentary lobe and passes to the oculomotor nerve on the same side.

When we consider the fact that in the Hexapoda the optic lobes are fused with the protocerebron, while in the crayfish



they are removed from the brain, we must conclude that the optic tracts homologize well. A comparison of the tracts found in the crayfish with those found by KENYON ('96) in the bee illustrates this statement.

*Fibers Related to the Antennulary Nerve.* The antennulary nerve of *Cambarus* has two prominent roots: the olfactory root arising from the olfactory lobe, and the deutocerebral root arising from the brain (fig. 14). On entering the brain the fibers of the olfactory root diverge and pass to the olfactory lobe (fig. 14, *Ol. T.*)

The deutocerebral root is related to the following intracerebral tracts.

*Antennulo-mesal Tract.* This is a narrow non-decussating tract which passes from near the meson to the antennulary nerve.

*Major Antennulary Tract.* This, the broadest of the antennulary tracts, passes direct from the antennulary lobe to the antennulary nerve of the same side (fig. 14, *M. Ant.*).

*Antennulary Commissure.* This commissure is situated near the opposite side of the brain from that on which the nerve enters (fig. 11, *Ant. C.*)

*Dorsal Antennulary Tract.* This tract passes in a broad curve from the dorsal tract nidus to the antennulary nerve (fig. 15, *D. Ant.*)

*Minor Antennulary Tract.* This is a small tract which passes, without decussating, from a nidus near the collar to the antennulary nerve (fig. 16, *Mi. Ant.*).

*Fibers Related to the Tegumentary Nerves.* In connection with the tegumentary nerve it has been possible to demonstrate the existence of the following tracts.

*Major Tegumentary Tract.* This is is a broad tract which passes direct from the tegumentary lobe to the tegumentary nerve (fig. 12, *M. T.*).

*Mesal Tegumentary Tract.* This is is a small tract which arises from a nidus situated near the meson on the opposite side of the brain from that on which the tegumentary nerve root is situated. It passes along parallel to the meson until

almost on a level with the nerve root, then passes laterad to the nerve. This tract does not decussate (fig. 12, *Me. T.*)

*Minor Tegumentary Tract.* This is a small tract which may easily be traced from the tegumentary nerve inwards (mesad) to near the meson. I have not been able to determine whether it terminates there or decussates to the other side (fig. 13, *Mi. T.*)

I have not been able to detect a commissure which is undoubtedly related to this nerve. However, between the antennary commissure and the roots of the antennary nerve there is a narrow commissure or decussation, the fibers of which can be traced to the vicinity of the roots of the tegumentary nerve; but it has not been possible to detect any of the fibers entering the nerve.

*Tracts Related to the Antennary Nerve.* It has been possible to demonstrate four tracts that connect with this nerve; the antennary commissure, the major antennary tract, the minor antennary tract, and the antenno-mushroom tract.

*The Antennary Commissure* arises from the cells of the ventral nidus and decussates to the nerve of the opposite side.

*Major Antennary Tract.* This tract arises from the ventral nidus and passes outwards (laterad) to the nerve of the same side.

*Minor Antennary Tract.* This tract passes from the latero-ventral nidus to the branch of the antennary nerve of the same side.

*Antenno-mushroom Tract.* This tract passes from the inner mushroom nidus to the nerve of the same side.

*Optico-olfactory Commissure or Fibrillar Arch.* This is a large and conspicuous commissure which connects the portions of the brain that lie adjacent to the roots of the mushroom bodies (figs. 3, 6, 9, 27). This is the homologue of the fibrillar arch (KENYON) of insects.

#### MUSHROOM BODIES.

The mushroom bodies are composed of two factors, cells and fiber tracts. The cells are minute bodies having small

nuclei and almost no cytoplasm. In this respect they resemble DEITER's corpuscles of the vertebrate brain. Compact masses of these cells crown stalks of nerve fibers and remind one of miniature mushrooms. In these nidi the cells are arranged in rows which radiate from the top of each stalk. In many insects each nidus is lodged in a cup-shaped structure known as a calyx. A cup-shaped calyx, however, is not a constant component of the mushroom bodies even in insects. KENYON has written ('96): "The bodies [calyx of the mushroom bodies] reach their highest development in the *Hymenoptera* and are much larger in the social wasps than in the honey bee. In *Blatta* the lateral walls of the cups are much reduced, and in the *Coleoptera* the cup-like form is scarcely recognizable, while in *Forficula* and *Acridum* the fibrillar substance only forms a broad plate. Even this is scarcely, if at all, recognizable in *Dytiscus*. In *Tabanus* and *Somomya* the four folds are reduced to two and in the former of these genera are scarcely to be distinguished by a comparison of their cells with those surrounding them."

#### *Stalks of the Mushroom-bodies.*

In the crayfish each mushroom nidus rests upon a tract of nerve fibers, bearing towards the tract the same relation that the pileus does to the stalk of the mushroom. The nidus surmounted tracts are known as the stalks of the mushroom bodies. In the crayfish these stalks of the same half of the brain converge and unite (figs. 22, 25). This is also the case in many insects, as may be seen by examining the brain of a larval butterfly (fig. 26) or by consulting KENYON's work on the bee. These peculiar mushroom nidi with their stalks are found not only in the crayfish but also in certain worms: i. e. *Nereis* (fig. 28), *Polynoe* (fig. 29), *Lepidonotus* (fig. 30). In these worms, however, instead of having two distinct mushroom nidi on each side, we find only one, or else one partly divided.

*Roots of the Mushroom-bodies.* From the point of union of the stalks of the mushroom-bodies arise two fiber tracts known as the stalks of the mushroom bodies. The more me-

dian of these, which is the narrower, passes inward (mesad) until past the border of the lobe in which it lies; then it turns mesodorsad until it nearly abuts against its fellow from the opposite side; then the two pass side by side for a short distance and then diverging pass into the optic nerve. The other tract passes outward and loses itself among the fibrils of the optic lobe.

These stalks are found not only in the crayfish (fig. 7), but also in the insects (fig. 26) and worms (fig. 28).

*Minute Structure of the Mushroom Nidi.* The cells of this region are peculiar in containing little or no extra-nuclear protoplasm. Fibers from these cells pass into the optic lobe and, branching dendritically, give it a speckled appearance.

It is thought that the comparative value of the facts discussed above can be best appreciated by consulting the following table:

COMPARISON OF THE MUSHROOM BODIES OF INSECTS, CRAYFISH AND WORMS.

Crayfish	Insects	Worms
Located in the supra-oesophageal ganglion	Located in the supra-oesophageal ganglion	Located in the supra-oesophageal ganglion
Four nidi of cells	Four nidi of cells (sometimes only two)	Two nidi of cells (sometimes each nidus is partially subdivided)
Cells of each nidus arranged in rows which radiate from a common base	Cells of each nidus arranged in rows which radiate from a common base	Cells of each nidus arranged in rows which radiate from a common base
Cells contain little or no extra-nuclear protoplasm	Cells contain little or no extra-nuclear protoplasm	Cells contain little or no extra-nuclear protoplasm
Fibers from the cells branch dendritically giving the brain near the cells a speckled appearance	Fibers from the cells branch dendritically giving the brain near the cells a speckled appearance	
Each nidus caps a stalk of nerve fibers	Each nidus caps a stalk of nerve fibers	Each nidus caps a stalk of nerve fibers
In the neighborhood we find: Central body, Procerebral bridge, Lower optic commissure, Optic chiasm, Fibrillar arch, Etc.	In the neighborhood we find: Central body, Procerebral bridge, Lower optic commissure, Optic chiasm, Fibrillar arch, Etc.	In the neighborhood we find: Central body

## CONCLUSIONS.

The purpose of this paper being not so much to make an exhaustive study of the brain as to carefully investigate the environment of the mushroom-bodies, especial stress has been placed upon the fiber tracts related to the mushroom bodies and to the intra-cerebral tracts of the cranial nerves, and certain tracts not directly related to these have been passed over without a word.

Histologically the supra-oesophageal ganglia of the decapods differ from those of the insects in lacking trachæ and in having the optic lobes separated from the brain; yet the evidence in favor of their being homologous structures is overwhelming.

The supra-oesophageal ganglion of the crayfish gives origin to five pairs of nerves.

The crayfish brain contains a central-body homologous to the central-body of the insect brain.

This central body is found, not only in the decapods but also in the lower crustacea and even in certain worms.

Histologically this central-body is a mass of fine fibrils.

This central-body receives fibers from several sources, yet all the preparations at my disposal militate against VIALLANES' assertion that fibers from this body radiate to all parts of the brain.

Like the insect brain, the supra-oesophageal ganglion of the crayfish contains a smaller structure resembling the central-body histologically, known as the procerebral bridge.

The internal structure of the crayfish brain is complicated; there are several cell-nidi and each nerve has related to it several fiber-tracts; but the principal cell-nidi and fiber-tracts homologize well with those of the hexapod brain.

Since the mushroom bodies of the crayfish and insects have the same histological structure, since they are situated in the same portion of the brain and since they are environed by at least five similar bodies, there seems to be no escape from

the conclusion that the mushroom bodies of the insects and crayfish are homologous.

The above table indicates that the worms also contain mushroom bodies in a lower stages of development than those of the insects.

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## EXPLANATION OF PLATES.

### REFERENCE LETTERS.

a.—Central portion of the olfactory lobe.

A.L.—Antennular Lobe.

Ant.C.—Tract of the antennular nerve.

Ant.L.—Antennary lobe.

Ant.N.—Antennary nerve.

A.O.T.—Anterior optic tract.

C.—Outer portion of the olfactory lobe.

C.B.—Central body.

C.M.—Cells of the mushroom nidi.

- D. Ant.*.—Dorsal antennular tract.  
*D. N.*.—Dorsal nidus.  
*D. L. T.*.—Dorso-lateral tract.  
*F. A.*—Fibrillar arch.  
*Ia. Ib. Ic. Id.*.—Lower optic commissure.  
*I. D. L.*.—Inferior dorsal lobe.  
*I. M. N.*.—Inner mushroom nidus.  
*L. V. N.*.—Latero-ventral nidus.  
*M. Ant.*.—Major antennular tract.  
*M. T.*.—Major tegumentary tract.  
*Me. T.*.—Mesal tegumentary tract.  
*Mi. Ant.*.—Minor antennular tract.  
*O. A. T.*.—Optico-arch tract.  
*O. C.*.—Optic chiasm.  
*O. Com.*.—Oesophageal collar.  
*O. M. N.*.—Outer mushroom nidus.  
*O. M. Nv.*.—Oculo-motor nerve.  
*O. M. T.*.—Optico-mushroom tract.  
*O. N.*.—Optic nerve.  
*Ol. L.*.—Olfactory lobe.  
*Op. L.*.—Optic lobe.  
*P. B.*.—Procerebral bridge.  
*P. L.*.—Pyriform lobe.  
*S. M.*.—Stalks of the mushroom-bodies.  
*T. L.*.—Tegumentary lobe.  
*T. N.*.—Tegumentary nerve.  
 All figures were drawn with the camera lucida.

## PLATE XXI.

- Fig. 1.* Diagram showing the lobes, nidi and nerves of the crayfish-brain.  
*Fig. 2-8.* Transverse sections through the crayfish brain.

## PLATE XXII.

- Fig. 9.* Transverse section through the crayfish brain.  
*Fig. 10-14.* Horizontal sections through the crayfish brain.  
*Fig. 15-17.* Longitudinal " " " " "

## PLATE XXIII.

- Fig. 18.* Longitudinal section through the crayfish brain.  
*Fig. 19.* Origin of optic nerves of the crayfish.  
*Fig. 20, 22, 23.* Sections through the mushroom bodies of the crayfish.  
*Fig. 24.* Cluster of nerve cells from the crayfish.  
*Fig. 21, 25.* Transverse sections through the crayfish brain.  
*Fig. 26.* " " " " brain of the *Cecropia* caterpillar.

## PLATE XXIV.

*Fig. 27.* Section through the brain of *Palæmonetes vulgaris* in the region of the mushroom bodies.

*Fig. 28.* Section through the brain of *Nereis*.

*Fig. 29.* " " " " *Polynœe*.

*Fig. 30.* " " " " *Lepidonotus*.

*Fig. 31.* " " " " *Limulus*.

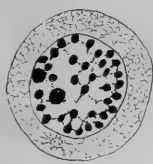
*Fig. 32.* Cell from the mushroom body of the crayfish.

*Fig. 33.* Section through the brain of *Polynœe*.

*Fig. 34.* " " " " *Branchipus*.



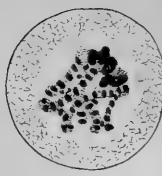
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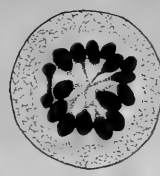
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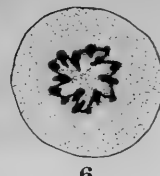
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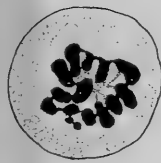
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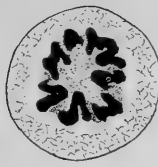
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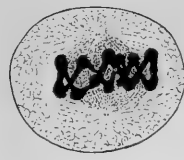
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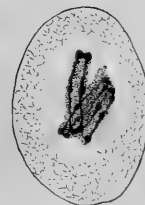
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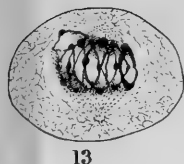
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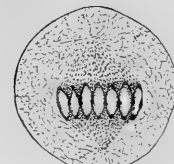
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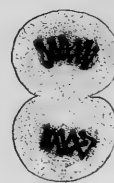
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FIG. 1

FIG. 2

FIG. 3

FIG. 4

FIG. 5

FIG. 6

FIG. 7

FIG. 8

FIG. 9

FIG. 10

FIG. 11

FIG. 12

FIG. 13

*a*

*a*

*b*

*a*

*b*

*a*

*b*

*a*

*a*

*b*

*a*

*a*

*a*



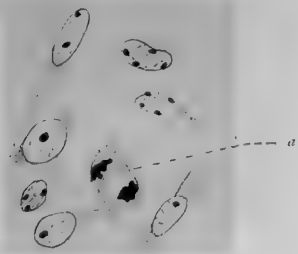


FIG. 14



FIG. 15

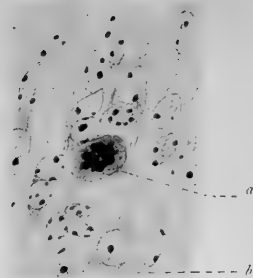


FIG. 16

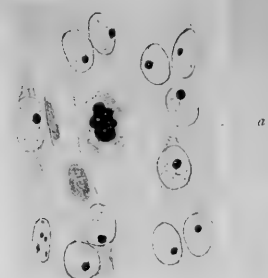


FIG. 17

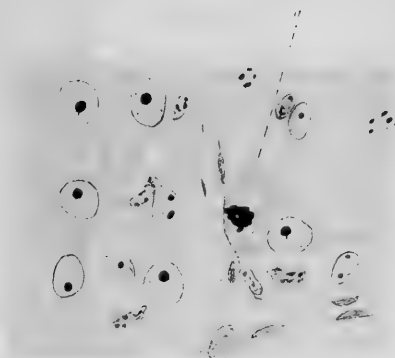


FIG. 18

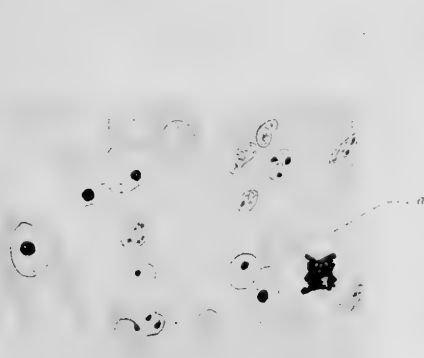


FIG. 19

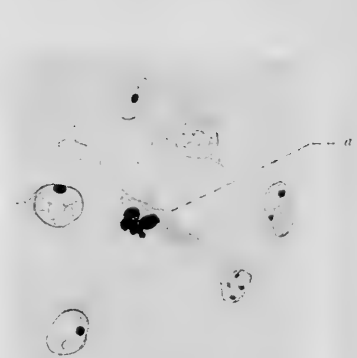
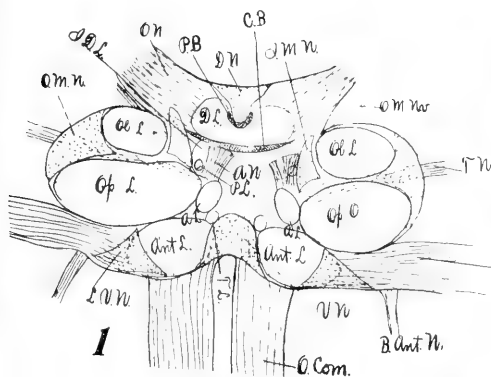
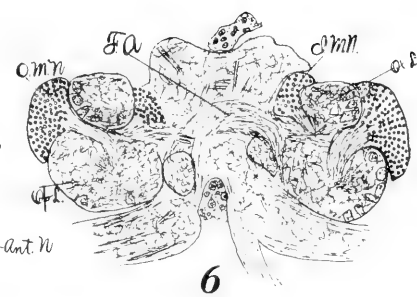


FIG. 20

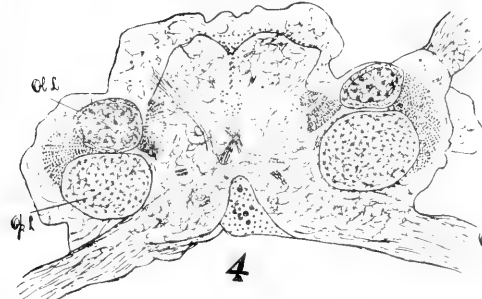




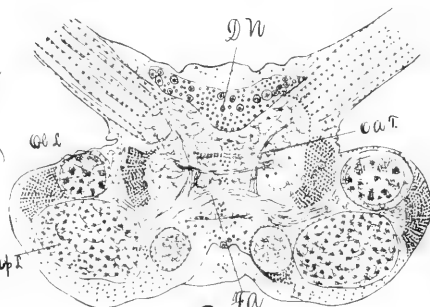
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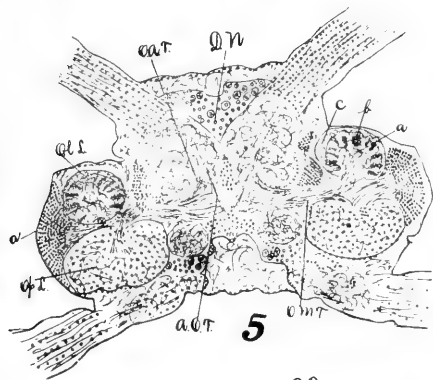
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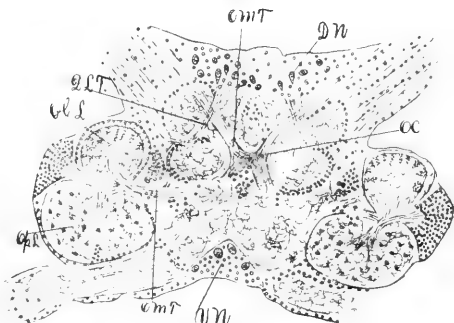
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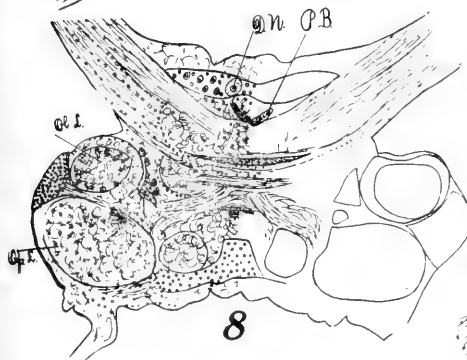
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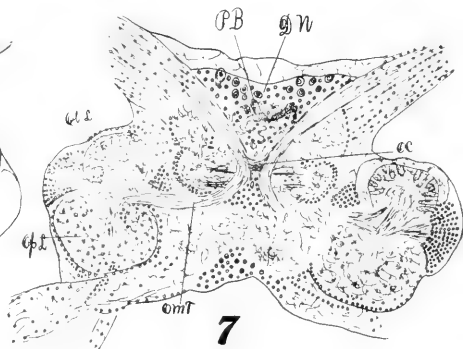
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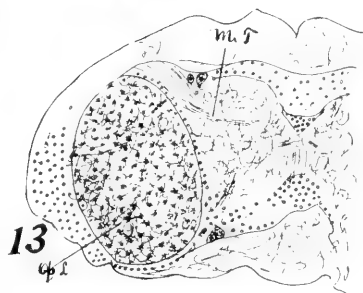
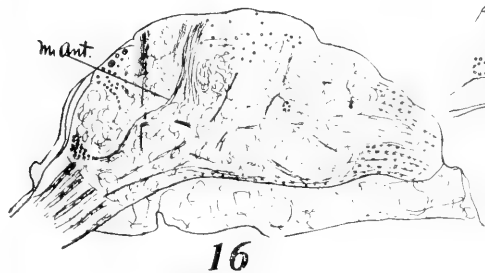
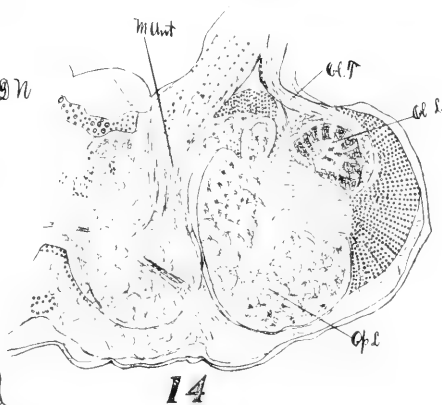
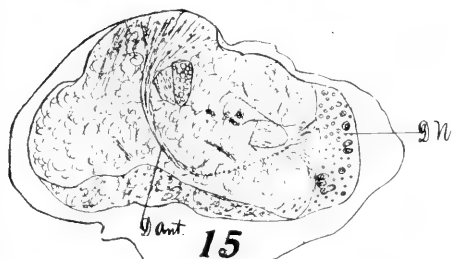
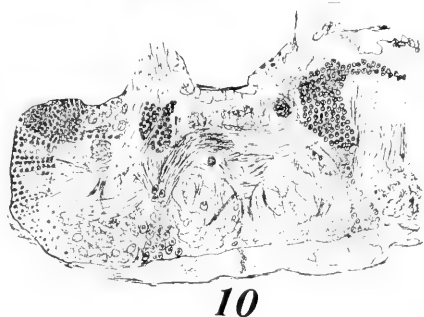
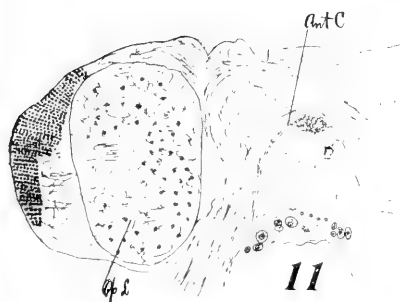
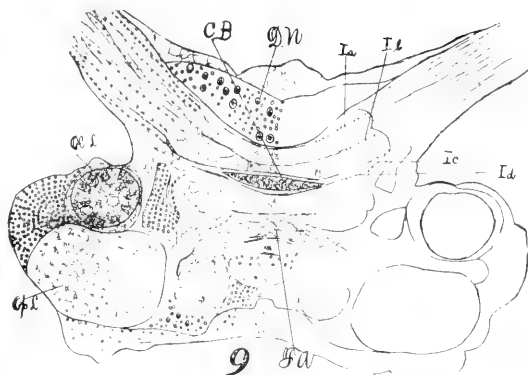
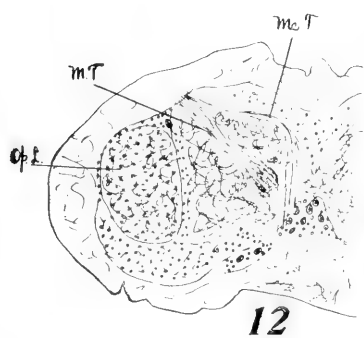


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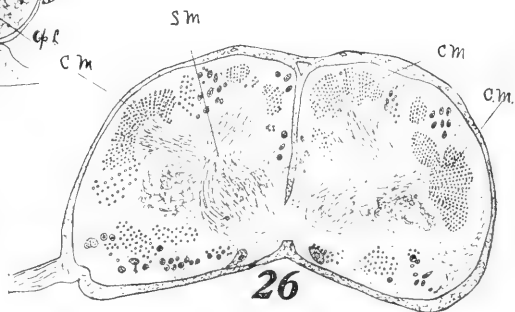
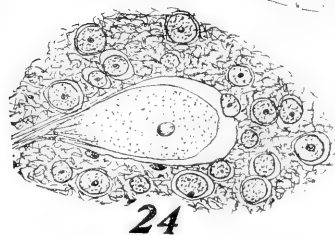
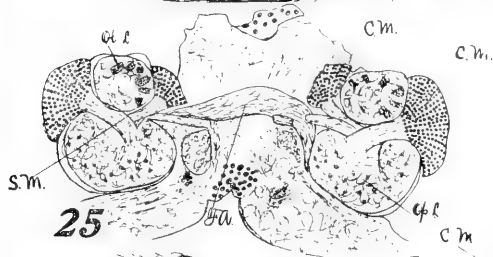
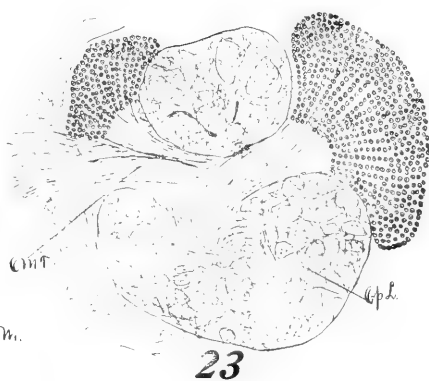
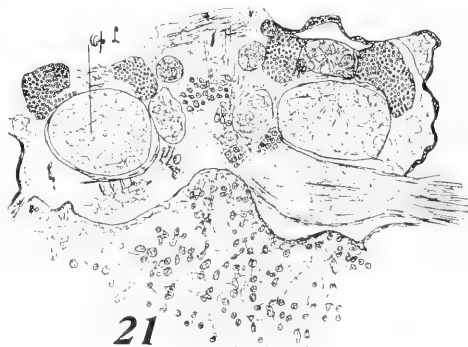
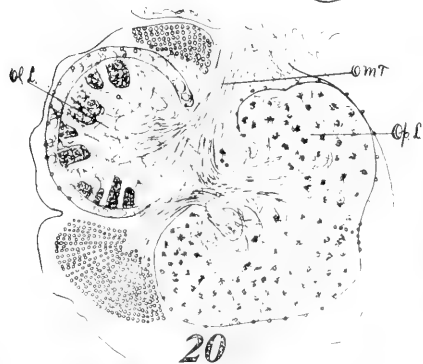
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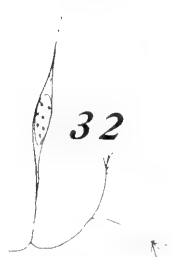
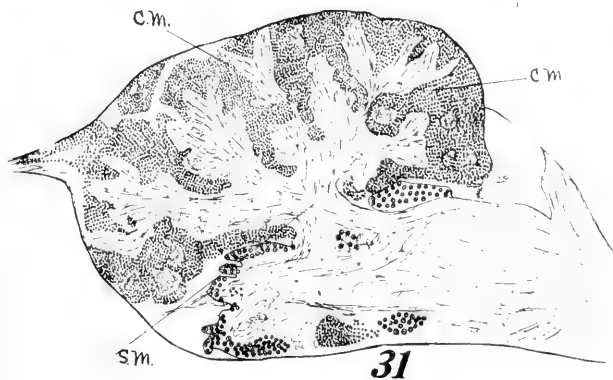
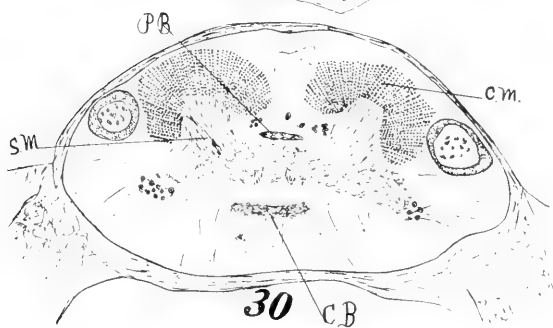
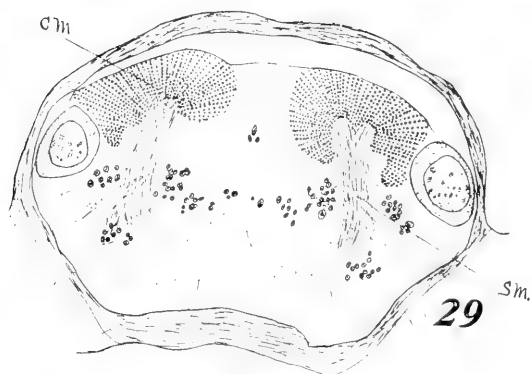
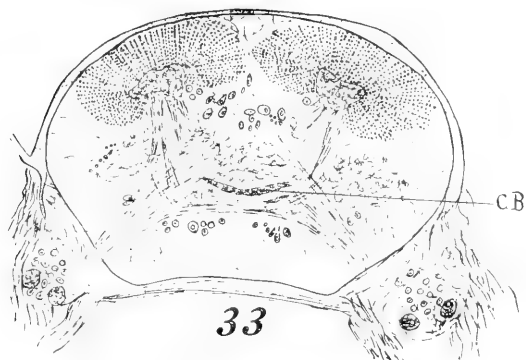














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### A BIBLIOGRAPHY OF THE LITERATURE ON THE ORGAN AND SENSE OF SMELL.

By H. HEATH BAWDEN.

The literature of the pathology of the organ and sense of smell—rhinoscopy and rhinology—is touched upon here only in its general bearings on structure and function. An exhaustive bibliography of this literature is to be found in the Index-Catalog of the Library of the Surgeon-General's Office, U. S. Army, under the articles: "Smell," "Nerve," "Canal," "Jacobson's Organ," "Rhinoscopy," "Nose," etc.; also in the Annual of the Universal Medical Sciences, edited by C. E. Sajous, 1894, IV, D, 1-102 and V, J, 32-35. Cf. also files of *Intern. Centralbl. f. Laryngol. Rhinol. etc.*; *Arch. f. Laryngol. u. Rhinol.*; and *Transac. Amer. Laryngol. Assoc.*

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The references fall naturally into two divisions, the literature on: (I) The Anatomy and Histology of the Organ of Smell, and (II) The Physiology and Psychology of the Sense of Smell.

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## LITERARY NOTICES.

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### REVIEW OF RECENT TEXT-BOOKS OF ANATOMY AND PATHOLOGY OF THE NERVOUS SYSTEM.

#### THIRD ARTICLE.

##### **Berkley's Mental Diseases.<sup>1</sup>**

This volume dedicated to Prof. HENRY M. HURD comes from a well-known worker on neurological topics. He introduces the book as follows "The absence from English medical literature of a comprehensive, practical work on mental diseases—one adapted to the needs of the busy practitioner, as well as to those of the student of psychiatry—has led the writer to prepare this treatise embodying a consideration of all the principal forms of psychical disturbance. Although it is evident, from the intrinsic nature of the subject, that such an attempt can be only partially successful, it is to be hoped that the book will add something to the certain knowledge of the practitioners, and render more accessible what has been heretofore almost an unknown territory of medicine."

This note which might surprise writers like SPITZKA, BEVAN LEWIS, MAUDSLEY, CLOUSTON, not to mention others less favored by reputation, invites a comparative review of modern attempts at writing on mental disorders. The explanation of the plan of the book is, however, better obtained from the title, and we shall review the book as representing a course in psychiatry for practitioners and students.

The book consists of three parts: 1. The anatomy and histology of the central nervous system (pp. 1-50); 2. General pathology (pp. 51-96); 3. The clinical forms of mental diseases (pp. 97-575). A very complete index is offered on pages 577-601.

The first part is in reality a summary of some of the present knowledge of the cortex cerebri, its circulation, membranes, vessels and lymphatics, neuroglia and nerve elements.

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<sup>1</sup> A Treatise on Mental Diseases, based upon the lecture course at the Johns Hopkins University, 1899, and designed for the use of practitioners and students of medicine. By HENRY J. BERKLEY, M. D., Clinical Professor of Psychiatry, the Johns Hopkins University, chief visiting physician to the City Insane Asylum, Baltimore. With frontispiece, lithographic plate and illustrations in the text. New York. D. Appleton & Co., 1900.

The second part consists in reality of an introduction, emphasizing the importance of heredity (especially for the "degenerative types of insanity") and of vascular derangement; the gross pathological anatomy and the "special pathology," dealing with the nerve-cell; and further, the "pathology of the cerebral arteries and veins" and "syphilitic vascular lesions."

The clinical section (part III) gives a sketch of classification (4 p.), the general etiology of insanity (pp. 101-108), general symptomatology (pp. 109-124) and general treatment (pp. 125-129).

The very plan of this general preparation of student and practitioner for the problems of the special clinical portion is open to several criticisms. 1. We may well plead for the busy practitioner, that he shall not be burdened with things which are of no avail to him or to psychiatry as it stands today. What interests a writer of a text-book on psychiatry need not belong to the psychiatry nor to the range of interests of the practitioner. From this point of view the greater portion of parts I and II are written *pro domo*, or for the students working in special laboratories. For the latter the scope of these parts is, however, too small and not systematic enough; and for him who knows little of laboratory work—practitioners so numerous that we cannot eliminate them—they are to some extent misleading and unintelligible.

2. The limitation of the writer's considerations to the cortex cerebri is arbitrary. We maintain that as far as we know anything about the nervous system in "mental diseases," we have not one on record which limits itself to the cerebral cortex, if it gives any lesions at all. If the cerebral cortex receives special attention, it ought not to be treated as one homogeneous thing, in these days of CAJAL and FLECHSIG and others, nor should one meet with descriptions of "the" nerve-cell.

3. In point of illustration and description and clearness the vascular disorders obtain an undue predominance; the few cases of pigmented and shrunken cells (plate V) are in remarkable contrast with the plate on vascular changes and the figures of the basal blood vessels and the cells in ricin-poisoning. Are we to be blamed for having expected some illustrative evidence of BERKLEY's types of cell degeneration (such as depigmentation)?

We do not want to leave this cortical part of psychiatry without a tribute to the presentation of the problem of cerebral circulation and the digest of much of BERKLEY's own work. We repeat, however, that to our own mind the question, What does a student of psychiatry

need in the way of general anatomical introduction? does not find a very good answer, nor the data of histo-pathology a lucid presentation.

This holds still more for the introduction into clinical psychiatry.

A classification in a text-book appears justified, if it helps the student to arrange the writer's ideas or the facts or, if possible, both. BERKLEY promises to follow KRAFFT-EBING in order not to add a further attempt; but he cannot resist the temptation of giving four groups:

1. Mental diseases without ascertainable pathological alteration of the brain substance.
2. Mental diseases sequential to ascertainable alteration of the cerebral substance.
3. Insanities due to inherited or acquired mental instability.
4. States of complete or incomplete retardation of the psychical (and physical) development.

I should be greatly distressed if I had to group my patients in such a manner, and to what extent would it help me?

In the general etiology of insanity, BERKLEY considers civilization and education (with special reference to the negro), brain-cell degeneration from overstrain (how demonstrable?), nationality, gender, age, and heredity, and alcohol as the most important of inciting causes—a very gloomy look into the prophylaxis, since, of all the things mentioned, alcoholism is the only one from which there is an escape, and perhaps the brain-cell degeneration, if it were not a *petitio principii*.

In the general symptomatology, due emphasis is laid on the necessity of a complete examination from a general medical point of view. The analysis of the mental symptoms is, however, very precarious. Many of the most valuable features for the purpose of a diagnosis of prognostic and not merely descriptive value, are not mentioned and are left as "heretofore almost an unknown territory." SOMMER and KRAEPELIN have lived in vain; and the literature which in other chapters is ample, limited to PARISH and REDLICH.

This may be the place for a comment on the omission of a short outline of psychological data which might well be considered more certainly a condition for a new psychiatry than the anatomy of the cortex. To avoid a poor psychology one ought not to invite the student or even a busy practitioner to avoid a careful treatment of the data which belong in the field of psychology. To do without some useful working hypothesis and working plan in the examination of mental disorders, is the same as to return to the old coughs and pulses in general medicine. Today it is far more necessary that a physician should learn to cope with the psychic data than even with the anatomy

of the cortex. Where shall he get it if not in a modern book on mental diseases? The anatomy he can get treated well enough in his handbooks of anatomy and physiology. But where is the psychology written by the physician of experience and for the needs of the physician?

It is to be hoped that a new edition will meet this need.

The special discussion of mental diseases follows time-honored principles, mainly the plan of KRAFFT-EBING. The refreshing breeze that has been going through psychiatry, since the stimulating, though daring, publication of KRAEPELIN's last editions, has had no effect on BERKLEY. He leaves the practitioner in ignorance of what most of us younger alienists deem to be the most important purpose of our work: to put in evidence the problematic feature of disease-entities unless they mean something from the point of view of etiology, course of development of symptoms complexes and nature of the termination, a standpoint admirably sketched by Dr. AUGUST HOCH in the *American Journal of Insanity*, October, 1900. Instead of that we get the traditional melancholias and manias and states of mental enfeeblement put together because they are "insanities without ascertainable alteration of the brain substance." Then comes the group "consecutive to" organic lesion of the cerebral substance, progressive paralysis, syphilitic insanity, the psychoses of old age, those following gross organic brain disease, the intoxication insanities (alcohol, opium, cocaine, and rarer poisons) and the insanities following bacterial, toxalbumic and autotoxic poisoning. In this chapter we find all those things put together in which the author would like to find an organic lesion. Puerperal insanities are treated here, although so many of them belong into other quarters and are only accidentally puerperal.

The third group is that of the psychic degenerate. What is gained by stamping all the forms treated here as degenerates is very difficult to see. BERKLEY might have been warned by the reserve of MAGNAN, who is the protector *par excellence* of the concept of degeneracy in insanity, even if he himself has never found an exception from his own rule in his practice. The chapter on periodic insanity abounds with similar claims of knowledge of the bearing of heredity. The psychoses accompanying the constitutional neuroses (neurasthenia is treated especially fully), imbecility and the psychoses of childhood take up considerable space.

To every part a long bibliographic list is added. All the articles show more than most books in English an effort to do justice to some of the literature. With all that, the articles make us more familiar with the scope of lectures than with the problems that confront one in a



hospital or which had best lead the practitioner and student. With many excellent traits, the lack of an easy grasp on the topic does not bring the book up to the standard of KRAFFT-EBING, and we doubt whether it reaches that of SPITZKA which, compared to BERKLEY's book is antiquated chiefly in matters of little importance to the practitioners and which in a new edition could easily incorporate many new acquisitions.

I should like to repeat what I expressed at the close of a review of Dr. PETERSON's book on mental diseases. We stand at a point in psychiatry at which it is particularly difficult to write a book which is up to date and clearly points the way to actual work in psychiatry and perhaps to problems of research. We have almost no research clinics in this country; hence the tendency to drift into beaten paths, lack of sense of proportion of what really occurs and is most stimulating for work in practice and in observation, and perpetuation of terminology of degeneracy and auto-intoxication and other topics of fascination, the valuation, of which belongs to the future and to hard work with facilities rarely offered today.

ADOLF MEYER.

#### Saunders' American Year-Book.<sup>1</sup>

The issue of the Year-Book for 1900 in two volumes met with such general approval from the profession that the publishers have followed the same plan with the Year-Book for 1901. This arrangement has a two-fold advantage. To the physician who uses the entire book, it offers an increased amount of matter in the most convenient form for easy consultation, and without any increase in price; while specialists and others who want either the medical or the surgical section alone, secure the complete consideration of their branch at a nominal sum, without the necessity of purchasing considerable material for which they have no special use. The section on Nervous and Mental Diseases in Vol. I, comprising 40 pages, is prepared by Dr. ARCHIBALD CHURCH, of Chicago. Some neurological papers are touched upon in other parts of the work, notably in the section devoted to Physiology.

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<sup>1</sup> The American Year-Book of Medicine and Surgery for 1901. A Yearly Digest of Scientific Progress and Authoritative Opinion in all branches of Medicine and Surgery, drawn from journals, monographs, and text-books, of the leading American and foreign authors and investigators. Arranged with critical editorial comments, by eminent American specialists. In two volumes—Volume I, including *General Medicine*, Octavo, 681 pages, illustrated; Volume II, *General Surgery*, Octavo, 610 pages, illustrated. Philadelphia and London: W. B. Saunders & Co. 1901. Per volume: Cloth, \$3.00 net; Half Morocco, \$3.75 net.

**Bianchi's Psychiatry.<sup>1</sup>**

Professor BIANCHI announces that his new text-book of Psychiatry will be wrought out largely on new lines, cutting loose so far as possible from the traditional and scholastic treatment. Part I, just off the press, comprises 170 pages, with 54 text-figures, and is devoted to general anatomical and physiological considerations, such as the fundamental laws of the evolution of mind in relation with the evolution of the nervous system, the plan, architectonic, anatomical and physiological, of the human brain, and its relation to psychic processes. Great stress will be laid upon the physiology and histology of the central nervous system, as furnishing the basis upon which the Psychiatry of today is to be constructed. The second part will serve as a general introduction to the clinical study of mental disease, and the third part, naturally much larger, will take up the systematic treatment of the several psychopathies. The second and third parts are promised within a few months and the whole will make a work of some 600 pages octavo, with many figures.

C. J. H.

**The Boehm-Davidoff-Huber Histology.<sup>2</sup>**

Many American histologists have regarded the German edition of the text-book of BÖHM and DAVIDOFF as the best manual in print. Our satisfaction in seeing this work translated and thus made available for English-speaking students is greatly increased by the fact that the American editor has made extensive additions which are on the same high plane of excellence as that of the German original. The more important additions are in connection with the ductless glands and the peripheral nervous system, particularly nerve endings in muscles, glands and other organs. Our readers, who have followed the series of articles on these subjects which Dr. HUBER has contributed to the JOURNAL OF COMPARATIVE NEUROLOGY during the past few years, will need no further testimonial to the value of the additions to the German text. The publishers are to be commended not only for an admirable example of book-making, but for the very reasonable price which they have put upon it.

C. J. H.

<sup>1</sup> Trattato di Psichiatria ad Uso dei Medici e degli Studenti, by PROFESSOR L. BIANCHI. Part I, Naples, Casa Editrice cav. Dott. V. Pasquale, 1901.

<sup>2</sup> A Text-book of Histology including Microscopic Technique, by A. A. BÖHM, M.D., and M. VON DAVIDOFF, M.D., edited with extensive additions to both text and illustrations by G. CARL HUBER, M.D. Authorized translation from the second revised German edition by H. H. CUSHING, M.D. Philadelphia, W. B. Saunders & Co., 1900. 500 pages, 351 illustrations, price \$3.50.

**Jahresbericht f. Neurologie und Psychiatrie.<sup>1</sup>**

This volume is apparently quite equal to the two preceding issues in completeness and general excellence, and is indispensable as an aid to the research workers in all departments of neurology.

**Ruffini's "Ultraterminal fibrils."**

After examining some preparations made by APATHY, showing neurofibrils, RUFFINI re-examined some old gold chloride preparations made from the muscles of the thenar eminence of man and showing motor nerve endings. RUFFINI observed no peculiarity of structure at the time of making these preparations; on re-examination, however, he found that in the greater number of cases there arose from one of the terminal expansions of the end-plate a very fine, longer or shorter fibril, which passed toward and between the neighboring striated muscle fibers. This fibril is always single, very fine, non-medullated and presents at irregular intervals distinct varicosities. In passing from one muscle to another, this fibril glides upon the sarcolemma and winds through the endomysium to reach the neighboring muscle fiber upon which it seems to terminate. Occasionally it seems to pass in its course through the contractile substance of a neighboring muscle fiber. This fine nerve fibril, which RUFFINI names the *ultraterminal fibril*, may end in a small, but distinct end-disc, which he considers a true termination, beyond which he was unable to trace any fibril; at times, no terminal enlargement was seen, but a short and very fine collateral branch was given off; these cases the author interprets as due to an imperfect reaction of the gold chloride; sometimes an ultraterminal nerve fibril ends in a small expansion, due to a dichotomous division of the end of the fibril, accompanied by characteristic terminal varicosities, constituting a small secondary end-plate. Examining one of these secondary end-plates under high power he was able to see an extremely fine, long, smooth fibril, showing no varicosities, whose mode of ending he was unable to determine. From these facts, RUFFINI draws the conclusion that the motor end-plate in man does not represent the true termination of the motor nerve, because there exists a demonstrable anatomical continuity between it and a non-medullated

<sup>1</sup> Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie und Psychiatrie. Herausgegeben von Dr. E. FLATAU und Dr. C. JACOBSON, Redigiert von Professor Dr. E. MENDEL. III. Jahrgang, Bericht über das Jahr 1899, Berlin, S. Karger, 1900.

<sup>2</sup> ANGELO RUFFINI and STEFANO APATHY, Sulle fibrille ultraterminali nelle piastre motrici dell'uomo. *Rivista di Patologia nervosa e mentale*, Vol. V, 1900.

fibril arising from it. RUFFINI has illustrated his minute description with seven figures, showing the varicose ultraterminal fibril, the fine collateral branches, the different modes of termination of the fibril and the long smooth secondary fibril, concerning the termination of which he is in doubt. APATHY, in discussing these observations of RUFFINI, dwells upon their importance as showing in a concrete case and that in man, that some of the supposed nerve terminations are not terminations, and that they may constitute a direct connection from one neurone to another. Comparing these results with those gained by himself in his work on neurofibrils, he believes that there are no natural nerve terminations; that the conducting path is continuous and comparable to the circulatory system.

DR. DE WITT.

### Histogenesis of Schwann's Sheath.<sup>1</sup>

In trying to stain the neurofibrils in the developing axis cylinders of embryos after the method of APATHY (gold chloride method), GURWITSCH found that, while the neurofibrils were not stained, the sheaths of SCHWANN (neurolemma) were stained, at a time when other known methods did not show their presence. His observations were made on the sciatic nerves of sheep embryos, removed at a time when the nerve fibers possessed as yet no medullary sheaths. At this stage the sciatic nerves consist of a number of secondary bundles, surrounded by a loose connective sheath, concentrically arranged, and each bundle is surrounded by a delicate sheath containing large nuclei. In cross-section the secondary bundles appear finely granular and contain few nuclei. A cross-section of such a nerve, stained after APATHY's gold method, shows the delicate sheaths of the secondary bundles stained a deep violet, nearly black, from which lamella-like processes pass into the interior of the bundles, similarly stained. The nuclei in the secondary bundles are associated with these lamellæ. Longitudinal and cross-sections of suitable stages show that the lamellæ above mentioned develop into tubular structures—the sheaths of SCHWANN.

The sheaths of SCHWANN are, therefore, of mesodermal origin, developed from mesodermal cells with lamellar processes. The close apposition of the sheath of SCHWANN and the medullary sheath is attained secondarily by the increase in thickness of the axis cylinder and the medullary sheath.

G. C. H.

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<sup>1</sup> DR. ALEXANDER GURWITSCH. Die Histogenese der Schwann'schen Scheide. *Archiv für Anat. und Phys. Anat. Abtheil.*, Heft 1 and 2, 1900.

**Histogenesis of Myelin Sheaths.<sup>1</sup>**

In this communication KOLSTER records his observations on the histogenesis of the myelin in nerve fibers of the central and peripheral nervous systems. The observations were made on embryos of *Salmo trutta* and *Sterna hirundo*. In these embryos the Anlagen of the peripheral nerves consist of small bundles of very fine fibrils which grow from the neural canal. At their first appearance they contain no nuclei, but are surrounded by a sheath consisting of a single layer of cells derived from the mesoblastic sheath of the neural canal. The development of the myelin sheath begins in the large nerve fibers of MAUTHNER; somewhat later in the smaller nerve fibers of the bundle within the neural canal. At this time and during the entire period of the development of the myelin within the neural canal, its supporting tissue consists of ependym cells and their processes. The myelination of the fibers of the nerve roots begins at a time when there are as yet no nuclei in them. The development of the myelin begins therefore before there is present a sheath of SCHWANN. It begins in that portion of the fiber nearest the cell body and proceeds peripheralwards. According to KOLSTER the sheath of SCHWANN takes no part in the development of the myelin, this is an ectodermal structure as is the neuraxis.

G. C. H.

**Structure of Corpuseles of Ruffini and Pacini.<sup>1</sup>**

SFAMENI gives a brief description of the different forms of corpuscles of RUFFINI which are found in the foot of the dog, cat and monkey and then passes to a more minute description of the internal structures of such corpuscles, which does not differ materially from that given by RUFFINI for man. The blood capillaries follow the course of the nerve trunks, forming a rete surrounding the nerve fibers, but not penetrating into the interior of the terminal nerve organs. The supporting tissue is formed of a few elastic fibers, with much white fibrous tissue. The sheath of HENLE of the nerve fibers enters the outer part of the

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<sup>1</sup> DR. RUD. KOLSTER. Beiträge zur Kenntniss der Histogenese der peripheren Nerven nebst Bemerkungen über die Regeneration derselben nach Verletzungen. *Beiträge zur pathol. Anat. und zur allgem. Path.*, Vol. 26, 1899.

<sup>2</sup> Relazione sulla Memoria Presentata dal DOTT. PASCUALE SFAMENI: Intorno agli organi nervosi terminali del RUFFINI e ai corpuscoli del Pacini studiati nelle piante e nei polpastrelli del cane, del gatto e della scimmia. *Atti della R. Accademia delle Scienze di Torino*. Vol. XXXV, 1899-1900.

supporting tissue and spreads out on the superficial surface of the spindle forming a sheath for it. In the supporting tissue, is found a reticulum formed of the axis-cylinders of the nerve fibers which, before entering the terminal nerve organ, have lost their sheath of HENLE and medullary sheath. The author studied accurately the granular substance which constitutes the fundamental part of the organ of RUFFINI; in it are found nuclei which are the true terminal elements of the nerve organ, destined to receive the impressions from the external world and transmit them to the axis-cylinders. The organs of RUFFINI found in the subcutaneous adipose tissue are deputed for the sense of pressure. The PACINIAN corpuscles are few in the foot of the dog; more abundant in the cat and most numerous in the monkey and in man. The author has found that they are innervated by a branch of the same nerve which by other branches innervates the organs of RUFFINI. Presenting in the dog and cat the usual structure of the PACINIAN corpuscle, they are more complex in the monkey and in man. For this reason, the author believes that they have a more highly differentiated function than that of the organs of RUFFINI, which are found in equal number and of the same structure in all these animals.

DR. DE WITT.

### The Psychology of Idiocy.<sup>1</sup>

This is not a study of particular cases or of the curiosities of idiocy, but an attempt to draw off, so far as this is possible, the general characteristics of the psychology of idiots and imbeciles and thus to make a portrait, not of this or that type, but the general type. After two general chapters devoted to an introduction and classification and to descriptive methods, the author studies successively, Perception of Sensations, Attention, Instincts, Feelings, Language, Intelligence, Will, Personality, and Responsibility. A series of twelve plates illustrates the writing and drawings of idiots.

C. J. H.

### de Fleury on Neurasthenia.<sup>1</sup>

Without attempting to go over ground of the classical works on neurasthenia and taking for granted their accounts of etiology, symptomatology and diagnostics, Dr. DE FLEURY has organized the data accum-

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<sup>1</sup> Psychologie de l'idiot et de l'imbécile, par le Dr. PAUL SOLMIER. Deuxième édition, revue, avec 12 planches hors texte. 1 vol. in-8° de la *Bibliothèque de philosophie contemporaine*, 5 fr. Paris, F. Alcan, 1901.

<sup>2</sup> Les grands symptômes neurasthéniques, by Dr. MAURICE DE FLEURY. Paris, F. Alcan, 1901, price 7 fr. 50.

ulated during ten years of observation upon neurasthenia with a view to adding to our knowledge of the nature and treatment. The titles of the leading chapters are as follows: La sensation de fatigue; L'appareil circulatoire chez les neurasthéniques; Les troubles du sommeil; Les troubles digestifs; Les troubles de l'excrétion urinaire et de la nutrition; L'asthénie génitale; L'état mental neurasthénique; Pathogénie générale; Traitement.

### Grasset's Manual of Diagnosis.<sup>1</sup>

This is the third of a useful set of brief manuals which Dr. GRASSET has published in the series *Les Actualités Médicales* for the clinician. The first is devoted to clinical anatomy of the nerve centers, the second to diagnosis of diseases of the spinal cord, and the final issue to diagnosis of diseases of the brain. He discusses the symptomology of the sensori-motor apparatus, the mechanisms of orientation and speech and the encephalic apparatus of circulation, nutrition, respiration and secretion. Diseases of hearing, taste and smell are passed over in silence. There are several very convenient diagrams and tables.

C. J. H.

### Saunders' Medical Hand-Atlases.<sup>2</sup>

In this Atlas the author has portrayed an instructive section of medicine which is usually extremely difficult of mastery by students and practitioners. The descriptive text comprises some 200 pages in six parts, devoted to (1) the Morphology of the Nervous System, (2) Development and Structure of the Nervous System, (3) Anatomy and Physiology of the more important Nervous Pathways, (4) General Pathology and Treatment, (5) Special Pathology and Treatment, (6) Autopsy Technique. While the text is rather too condensed to serve alone as introductory text-book for medical classes, the plates will serve

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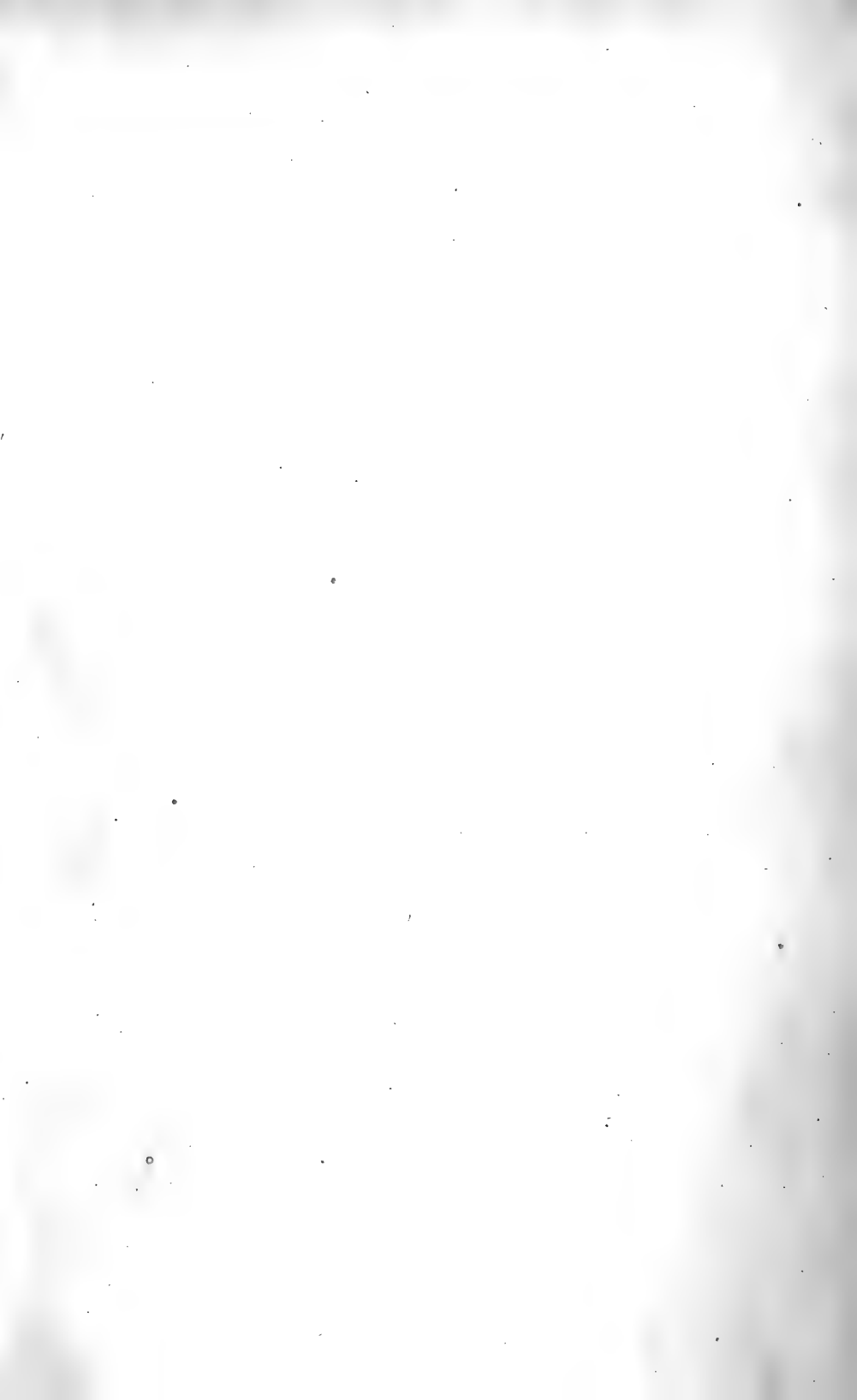
<sup>1</sup> Diagnostic des Maladies de l'Encéphale, par le Docteur GRASSET, professeur de clinique médicale à l'Université de Montpellier. 1 vol. in-16 de 96 pages, avec 6 figures, cartonné, fr. 50. (Librairie J.-B. Baillière et fils, 19, rue Hautefeuille, Paris, 1901.)

<sup>2</sup> Atlas and Epitome of the Nervous System and Its Diseases. By PROFESSOR DR. CHR. JAKOB of Erlangen. From the Second Revised German Edition. Edited by EDWARD D. FISHER, M.D., Professor of Diseases of the Nervous System, University and Bellevue Medical College, New York. With 81 plates and copious text. Philadelphia and London: W. B. Saunders & Co., 1901. Cloth, \$3.50 net.

admirably to illustrate such a course and both alike will be of value to the practitioner who desires to recast his neurological knowledge in accordance with recent teachings. There are occasional slips, as on p. 26, after correctly defining the neurone as the "nerve-cell with its entire nerve process," we read that the peripheral sensory neuron "has its cell approximately in the middle of its course;" but in general text and illustrations are well chosen, and the work as a whole can be cordially commended.

C. J. H.











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